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SUBFOSSIL MAMMALS FROM THE GÓMEZ FARÍAS REGION AND THE TROPICAL GRADIENT OF EASTERN MEXICO

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In the spring of 1953 Byron E. Harrell and P. S. Martin collected superficial animal remains at three cave localities in the Sierra Madre Oriental of southwestern Tamaulipas. Locally, the mountains are sufficiently humid to support small, isolated patches of Cloud Forest and Tropical Evergreen Forest (Martin, 1958). At this latitude, 23° north, these two tropical plant formations appear to reach their limit. In recent years four faunal papers on mammals of southern Tamaulipas have appeared, each reporting certain tropical species unknown at higher latitudes (Baker, 1951; Goodwin, 1954; Hooper, 1953; de la Torre, 1954). Southern Tamaulipas appears to be of primary significance in the Gulf lowlands faunal gradient, a system extending from southern Veracruz to southern Texas. In the lowlands of eastern Mexico many of the dominant tropical American taxa reach their range limits. We seek to define the northeastern section of this gradient with regard to tropical mammal faunas, to relate it to shifts in vegetation and to indicate the relative importance of the Gómez Farías region as a faunal terminus. The Gómez Farías region is defined as the area from 22°48′ to 23°30′ north latitude and 99° to 99°30′ west longitude, or approximately the rectangle enclosed by the towns of Llera, Jaumave, Ocampo and Limon.

In establishing the presence of eight species known in the Gómez Farías region only from the skeletal remains, and in extending the altitudinal or ecological ranges of others, the present collection supplements previous reports. It indicates the value of using owl pellet deposits as a cross check on standard trapping technique.

DESCRIPTION OF DEPOSITS

Cretaceous limestones comprising the precipitous east slope of the Sierra Madre Oriental near the village of Gómez Farías are severely folded. Under torrential summer rains they have eroded into very rough karst terrain with virtually no surface drainage. Caves and sink holes, a characteristic of karst, are a common feature. Most do not appear to be inhabited by bats or owls. Of those that are, the constant high humidity and frequent flushing from

percolating rainwater apparently prevent accumulation of deep bone or guano deposits. Large bat colonies numbering thousands of individuals occur in Tropical Deciduous Forest in the Canyon of the Río Boquilla, 8 km. southwest of Chamal, and in a guano cavern at El Abra, 8 km. northeast of Antiguo Morelos. However, no colonies of similar size have been found in the more humid portions of the Gómez Farías region.

Of approximately thirty caves and sink holes explored near Gómez Farías, material from three is represented in our collection. All occur in the mountains west of the village of Gómez Farías, latitude 29°03′ north, longitude 99°09′ west, and within 16 km. of each other (see Table 1). The following information will serve to characterize them:

1. Paraiso. Aserradero del Paraiso is the name of a small sawmill located in Tropical Evergreen Forest 13 km. north-northwest of Chamal. A narrow ravine about 1 km. south of the sawmill harbors several caves, including a deep, wet grotto with permanent water. On the sloping floor of a small

TABLE 1.—*Mammals from cave deposits in the Gómez Farías region (numbers refer to anterior skull parts identified)*

	PARAISO	RANCHO DEL CIELO	INFERNO
Distance from Gómez Farías:	13 km. SW	6 km. NW	7 km. W
Elevation in meters:	420	1050	1320
Vegetation type:	Tropical Evergreen Forest	Cloud Forest	Cloud Forest
Didelphis marsupialis	—	—	1
Marmosa mexicana	—	—	18
Cryptotis pergracilis	3		
Cryptotis mexicana	—	1	10
Chilonycteris parnellii	1		
Enchisthenes harti	—	—	1
Artibeus cinereus	—	3	
Centurio senex	—	—	1
Eptesicus fuscus	1		
Lasiurus cinereus	—	—	1
Antrozous pallidus	1		
Sylvilagus floridanus	1		
Glaucomys volans	1	1	12
Liomys irroratus	1		
Reithrodontomys mexicanus	—	2	5
Reithrodontomys megalotis	—	—	1
Baiomys taylori	1		
Peromyscus boylei	—	1	17
Peromyscus pectoralis	—	—	2
Peromyscus ochraventer	—	—	7
Oryzomys alfaroi	3	—	5
Sigmodon hispidus	29		
Neotoma angustapalata	9	1	17
Total identifications	51	9	98

dry cave on the west wall of this ravine many scattered (apparently water-transported) small bones were found.

2. Rancho del Cielo. A small sink and cave several hundred meters east of this important Cloud Forest collecting locality contained a few bat remains and fresh owl pellets.

3. Inferno (also designated Infernillo). A rather large cave adjacent to an abandoned sawmill of this name is located in upper Cloud Forest roughly 2 km. south of the mill settlement called La Gloria. Abundant pellet remains were found on a dislodged boulder just inside the cave mouth.

All the caves are surrounded by heavy forest, much of it recently lumbered. Jagged, shrub-covered or almost bare karst ridges and pinnacles confine the areas of tall forest to valleys, pockets and gentle slopes. A more complete description of the Gómez Farías region is in preparation (Martin, 1958).

Although the barn owl, *Tyto alba*, occurs in a very large cavern at El Abra north of Antiguo Morelos, the only raptor definitely known to roost in caves in the Gómez Farías region is the wood owl, *Ciccaba virgata*. While it is possible that certain non-volant mammals died from other causes, all skeletal remains of these, and perhaps even some of the bats, can be ascribed to *Ciccaba*.

Cave records do not make ideal locality data, especially when information on ecological or altitudinal distribution is sought. We assume that the forest types and the elevation in the immediate vicinity of each cave represent the habitat in which the owls fed, but this is by no means certain. The hunting range and nocturnal movements of *Ciccaba* are unknown.

There is no stratigraphic evidence for assuming that any material is older than very recent. Limestone deposit on certain bones may represent the concretion of a single rainy season.

SYSTEMATIC TREATMENT OF THE MAMMALS

We emphasize first that only a fraction of the mammalian and none of the bird bones have been identified. Very little attempt has been made to identify any of the post-cranial elements, and in the case of the cricetine rodents only the best of cranial material could be identified with any confidence. Particular difficulty was encountered with lower jaws of cricetines, even when teeth were present. As a result, determinations in this group are considered less reliable than in the others. In particular this applies to the *Peromyscus–Baiomys–Reithrodontomys* group of genera, in which not only specific but also good generic characteristics were hard to find in most of the material. Size, molar form, palatal morphology and shape of the zygomatic plate were found to provide the most useful taxonomic characters in this subfamily.

In many cases a closely adhering limestone drip deposit was present and was sometimes difficult to remove without damaging the underlying bone. No attempt has been made to identify subspecies. In our opinion the theoretical requirements of population sampling and measurement, as employed in sub-

specific identification, are not met in any but perhaps the best fossil material. For the following species determinations Koopman alone is responsible.

Didelphis marsupialis.—Inferno: one rostral fragment of a young individual. Previously recorded from Gómez Farías (Hooper, 1953).

Marmosa mexicana.—Inferno: three rostral fragments and 15 mandibles. On the basis of dentition, these are clearly opossums, but of the Middle American genera of Didelphidae, all but *Marmosa* are much too large. Of the four species of this genus occurring north of Panama, all but *M. mexicana* differ from the subfossil material either in larger size or greater development of a precondylar crest on the outer side of the mandible. The species has not previously been recorded north of Jalapa, Veracruz.

Cryptotis pergracilis.—Paraiso: one rostrum and two mandibles. Restriction to the family Soricidae and the genus *Cryptotis* may be made on the basis of dentition. In eastern Mexico north of the Isthmus of Tehuantepec (states of Tamaulipas, San Luis Potosí, Hidalgo, Puebla and Veracruz) the following six species of *Cryptotis* are known: *C. parva, C. pergracilis, C. obscura, C. micrura, C. mexicana* and *C. nelsoni.* All except *C. parva* and *C. pergracilis* may be ruled out on the basis of larger size. While clear-cut cranial differences between the latter two species appear to be absent, the eastern race of *pergracilis, C. p. pueblensis,* has a somewhat deeper nasal emargination of the rostrum than the southwestern race of *parva, C. p. berlandieri.* Though slightly broken anteriorly, the subfossil rostrum appears to have a nasal emargination somewhat closer to that of *C. pergracilis pueblensis* than to that of the two Tamaulipan specimens of *C. parva berlandieri* recorded by Goodwin (1954). However, no direct comparison of the Paraiso specimens with *C. pergracilis pueblensis* was made, but only with a sketch. Unfortunately our material seems inadequate to solve the problem of specific status, i.e., are *C. parva* and *C. pergracilis* sympatric in southern Tamaulipas, do they integrade through a narrow hybrid zone, or is there a more complex arrangement?

The northernmost previous record of *C. pergracilis* is Platanito in San Luis Potosí.

Cryptotis mexicana.—Inferno: six rostra, four mandibles, and three humeri; Rancho del Cielo: one rostrum. Specimens were trapped at the latter locality (Goodwin, 1954).

Chilonycteris parnellii.—Paraiso: one mandible. Goodwin (1954) records a series from El Pachon. As Koopman (1955) has pointed out, the mainland *C. rubiginosa* and the West Indian *C. parnellii* are almost certainly conspecific. Since Koopman believed that *C. parnellii* Gray had several months priority over *C. rubiginosa* Wagner, the combined species was called *C. parnellii.* De la Torre (1955) has shown that this is not the case and, finding no way of determining which name was published first, recommended: "In the absence of conclusive evidence, the better known and more widely used name *rubiginosa* should be retained."

Unfortunately, if there is no clear priority, the law of the first reviser would

seem to hold, in this case the first to use one of the two names to include both forms, i.e., Koopman (1955). It is not legally possible to withdraw from this position. Therefore it appears that *C. parnellii* must stand as the name assigned to both mainland and West Indian large *Chilonycteris*.

The question of nomenclature should not obscure the more significant taxonomic conclusion that a single species is involved.

Artibeus cinereus.—Rancho del Cielo: two partial skulls, one lower jaw. De la Torre has also recorded this species from Rancho del Cielo.

Enchisthenes harti.—Inferno: one partial skull. The short broad rostrum and characteristic molar pattern rule out all American bats outside the Stenoderminae. Of the Middle American stenodermines, only *Uroderma bilobatum*, *Vampyrops helleri* and *Enchisthenes harti* agree with the Inferno skull in size and dental formula (i^2 o^1 p^2 m^3). Both *Uroderma* and *Vampyrops*, however, have rostra considerably longer than that of the subfossil skull. On the other hand, there is close resemblance to skulls of *Enchisthenes* from Honduras and Ecuador. De la Torre (1955) has recently summarized the known records, specimens from Ciudad Guzman in Jalisco being the closest to Tamaulipas geographically. Four other localities extend the distribution south to Trinidad and Ecuador.

Centurio senex.—Inferno: one rostrum. Of all the North and Middle American bats, only *Centurio senex* agrees with the subfossil skull in dental formula (i^2 c^1 p^2 m^3) and in the palate being more than twice as wide as it is long. The Inferno rostrum resembles a skull of *Centurio senex* in all important respects. De la Torre (1954) recorded a single specimen from Pano Ayuctle.

Eptesicus fuscus.—Paraiso: one mandible. Several characters of this bone immediately narrow the field considerably. These are mandibular length, tooth size, dental formula (i_3 c_1 p_2 m_3), molar pattern and height of the coronoid process. This leaves us with only two North and Middle American species, *Eptesicus fuscus* and *Dasypterus intermedius*. Of these, *Dasypterus* may be ruled out on the basis of its more robust mandibular ramus. Comparison of the Paraiso mandible with *Eptesicus fuscus* reveals no important differences. I have been able to find no other records of this bat in Tamaulipas, the nearest localities being Río Ramos in Nuevo León to the west (Davis, 1944) and Cañada Grande in San Luis Potosí to the southwest (Dalquest, 1953). Good series from Tamaulipas, if they could be obtained, should show integradation between *E. f. fuscus* and *E. f. miradorensis*.

Lasiurus cinereus.—Inferno: one nearly complete skull. All other species of North and Middle American bats may easily be excluded from consideration on the basis of size, rostral shape and dental formula (i^1 c^1 p^2 m^3). It matches *L. cinereus* closely. Since this bat is migratory, it is impossible to say whether this individual belonged to a resident population or was merely a winter visitor. The nearest previous records are Matamoros in northern Tamaulipas (Miller, 1897) and El Salto in eastern San Luis Potosí (Dalquest, 1953).

Antrozous pallidus.—Paraiso: one partial lower jaw. Mandible and tooth

size, molar pattern and dental formula (i_2 c_1 p_2 m_3) rule out all North and Middle American bats except *Promops centralis* and *Antrozous*. *Promops* may be excluded by the quite different appearance of the labial surface of the coronoid region. Of the two species of *Antrozous* recognized by Orr (1954), *A. bunkeri* is distinctly larger than the Paraiso mandible. *A. pallidus* resembles it in all respects. The University of Michigan Museum of Zoology has six specimens from Tula, which were mentioned by Orr (1954).

Sylvilagus floridanus.—Paraiso: one maxillary fragment of a young individual. Goodwin (1954) records the species from Gómez Farías, Pano Ayuctle and Chamal.

Glaucomys volans.—Inferno: two palatal fragments, ten mandibles; Rancho del Cielo: one mandible; Paraiso: one mandible. From the dental formula (i_1 c_0^0 p_1^2 m_3^3) these specimens are clearly referable to the Sciuridae, of which all northeastern Mexican species except *Eutamias bulleri, E. dorsalis* and *Glaucomys volans* are clearly too large. In *Eutamias*, however, the mandible is much less deep than in the Tamaulipas material. The latter bears a convincing resemblance to *G. volans*. The nearest locality from which the species had previously been obtained is Santa Barbarita in San Luis Potosí (Dalquest, 1953).

Liomys irroratus.—Paraiso: one maxillary fragment. Goodwin (1954) records a series from Pano Ayuctle.

Oryzomys alfaroi.—Inferno: four maxillary fragments, one partial skull; Paraiso: three mandibles. Goodwin (1954) and Hooper (1953) have each recorded the species from Rancho del Cielo.

R. (Reithrodontomys) megalotis.—Inferno: one partial skull. Identification of this fragment is tentative. The species has already been recorded from Rancho del Cielo by both Goodwin (1954) and Hooper (1953).

R. (Aporodon) mexicanus.—Inferno: five partial skulls; Rancho del Cielo: two partial skulls. The species has been recorded previously from Rancho del Cielo by Goodwin (1954) and Hooper (1953).

Peromyscus boylei.—Inferno: two partial skulls, 15 maxillaries; Rancho del Cielo: one mandible. The species is recorded by Goodwin (1954) from both Rancho del Cielo and Rancho Viejo.

Peromyscus pectoralis.—Inferno: one partial skull, one maxillary. It has been recorded by Goodwin (1954) from both La Joya de Salas and 2 km. west of El Carrizo.

Peromyscus ochraventer.—Inferno: one partial skull, six maxillaries. The species has been recorded from Rancho del Cielo by both Goodwin (1954) and Hooper (1953).

Baiomys taylori.—Paraiso: one mandible. Goodwin (1954) and Hooper (1953) have recorded it from Pano Ayuctle.

Sigmodon hispidus.—Paraiso: one rostral half, ten maxillaries, two premaxillaries, three braincase elements, 16 mandibles. The species has been recorded from Pano Ayuctle by Goodwin (1954) and Hooper (1953).

Neotoma angustapalata.—Inferno: four partial rostra, five maxillaries, eight

mandibles; Rancho del Cielo: one maxillary; Paraiso: one maxillary fragment, two premaxillaries, six mandibles. There is also a great deal of additional *Neotoma* material from Inferno that probably belongs here, but which has not been specifically identified. Both Goodwin (1954) and Hooper (1953) list specimens from Rancho del Cielo and El Pachon although, as Hooper points out, the precise status of *N. angustapalata* and its various southern Tamaulipas populations is far from clear. At the present time this name appears to be something of a "catch-all." It is felt, however, that a revision should be based on entire specimens rather than on skeletal fragments.

FAUNAL COMPARISONS AND THE STATUS OF GLAUCOMYS

The identifications summarized in Table 1 represent total number of anterior skull elements and *not* total number of individuals, which may be somewhat less. Although such data do not lend themselves to close quantitative inspection, we feel that the faunas sampled near Inferno and Paraiso reveal important differences. Two quite different habitats, Cloud Forest and Tropical Evergreen Forest, are represented. It would be surprising if the faunas were qualitatively similar. *Peromyscus*, the dominant genus comprising 27 per cent of the Inferno deposits, is unrepresented at Paraiso. In turn, *Sigmodon*, which comprises 57 per cent of the material obtained at Paraiso, is absent from Inferno. Such a discrepancy may reflect an ecological shift in the dominant cricetine form. Other rather common species which appeared only in the Cloud Forest caves include: *Marmosa mexicana* (18%), *Cryptotis mexicana* (10%) and *Reithrodontomys mexicanus* (5%). One genus, *Neotoma*, occurs at both localities with a relatively constant frequency, 17–18 per cent.

Within the Gómez Farías region the following are known only from their skeletal remains: *Marmosa mexicana, Cryptotis pergracilis, Chilonycteris parnellii, Enchisthenes harti, Eptesicus fuscus, Lasiurus cinereus, Antrozous pallidus* and *Glaucomys volans*. Presence of the latter is perhaps of greatest interest. In Middle America flying squirrels are very poorly known, presumably the result of their nocturnal and arboreal habits rather than an inherent scarcity. We are aware of ten other locality records between Chihuahua and Honduras, each represented by one or two specimens. In the Gómez Farías region remains of *Glaucomys* appeared at each cave locality, suggesting a general range through humid forest, both Cloud Forest and Tropical Evergreen Forest, between 420 and 1,320 meters. To our knowledge *Glaucomys* has not previously been collected in lowland tropical forests (below 1,000 meters).

THE LOWLAND TROPICAL GRADIENT IN EASTERN MEXICO

We might imagine a lowland tropical fauna to decline with increasing latitude at a rather regular rate. However, in reality the environment and fauna undergo a series of discrete changes, stepwise (see Fig. 1). In eastern Mexico four major tropical lowland vegetation types are represented. From south to north they terminate in the following sequence: Rainforest, Tropical Ever-

green Forest, Tropical Deciduous Forest and Thorn Forest (Leopold, 1950). Each terminus is marked by a steepening of the faunal gradient.

In defining the lowland tropical fauna we have excluded those genera with distributional centers in temperate montane habitats or of limited lowland tropical ranges, e.g., *Idionycteris, Neotoma, Sciurus, Sigmodon* and *Baiomys*. On the other hand, some of the species selected may range into montane habitats or reach temperate latitudes, such as *Marmosa mexicana* and *Didelphis marsupialis*. In general the species listed in Table 2 are of wide distribution in lowland tropical America. Although they occupy tropical environments of the Mexican escarpment and coastal plain, we exclude *Baiomys* and *Sigmodon* because their phylogeny indicates a north temperate origin and in the case of *Baiomys* because it does not range extensively into Central America. Clearly the question of "tropicality" can be vexing. As one might expect the bats have much more extensive ranges than the small terrestrial mammals. The faunas of Trinidad and southern Tamaulipas share 18 species of bats, but none of rodents.

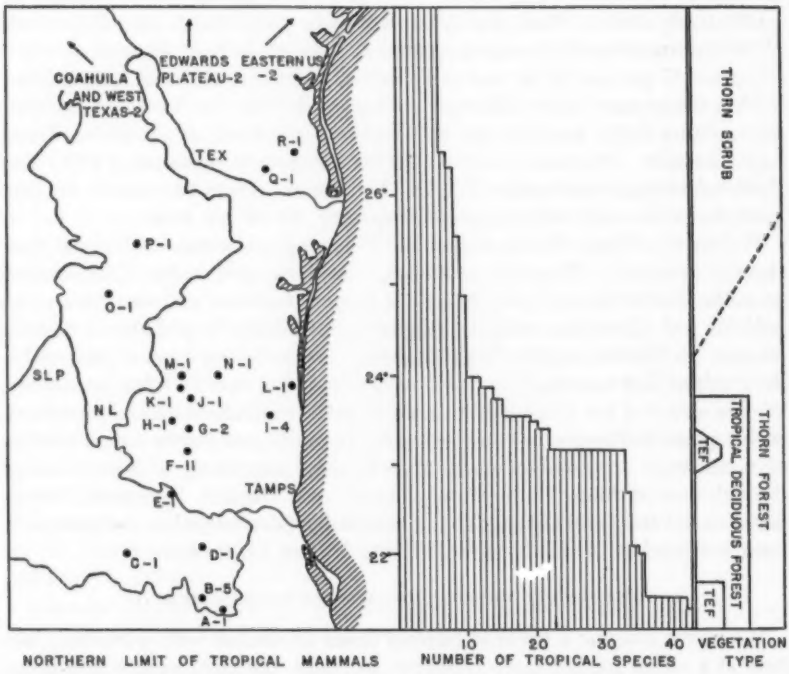

FIG. 1.—Relationship between lowland tropical mammals and latitude in northeastern Mexico. Known range limits for 43 species listed in Table 2 are shown on the map. Major vegetation types are indicated at the right. Tropical Evergreen Forest is abbreviated to TEF.

The general relationship between vegetation, latitude and tropical fauna is shown on Fig. 1. In southern Tamaulipas a rapid "thinning" of tropical forms is evident. Between 23° and 24° north latitude the following 17 genera find their range limits: *Philander, Marmosa, Chilonycteris, Pteronotus, Micronycteris, Macrotus, Glossophaga, Sturnira, Artibeus, Enchisthenes, Centurio, Natalus, Rhogeesa, Molossus, Heterogeomys, Eira* and *Mazama*. At this latitude (24° north) the Tropical Deciduous Forest, well developed and widespread east of the Sierra de Tamaulipas and the Sierra Madre Oriental, disappears. Small, perhaps relict, stands of Cloud Forest and Tropical Evergreen Forest in the Gómez Farías region also enrich the environmental opportunity for tropical mammals. However, these habitats, especially the Tropical Evergreen Forest, are more extensive in southeastern San Luis Potosí and northern Veracruz.

In this region seven genera terminate: *Carollia, Tamandua, Coendou, Cuniculus, Potos, Galictis* and *Ateles*. Although the vegetation near Xilitla, San Luis Potosí, has been designated as Rainforest, it seems preferable to reserve that term for the more luxuriant forests of southern Veracruz with their short dry season. Lowland tropical forests near Xilitla appear taller and richer than those of southern Tamaulipas; however, the area has suffered a long history of intensive Huastecan agriculture. Almost certainly the primeval fauna of southeastern San Luis Potosí included a larger number of tropical genera at their northern limit.

While we have not attempted to represent tropical distributions and plant formations south of San Luis Potosí, the following genera or subgenera approach their northern limit in southern Veracruz: *Caluromys, Vampyrum, Rhynchiscus, Centronycteris, Mimon, Chrotopterus, Hylonycteris, Chiroderma, Alouatta, Tylomys, Dasyprocta, Tayassu, Tapirella* and *Jentinkia*. Is there a relationship between these and the northern limit of Rainforest (see Leopold, 1950)?

Extending from central Tamaulipas northward to Nuevo León and southern Texas is a rather barren Thorn Forest and Thorn Scrub. Gradually these arid habitats lose their tropical character as the Rio Grande Valley is approached. By comparison with plant formations to the south, this environment is poor in tropical fauna. The shift from tropical to temperate thorn scrub involves no sharp faunal boundary among the mammals. *Oryzomys couesi* and *Liomys irroratus* are among the forms reaching southern Texas. At this latitude the herpetological fauna includes such tropical genera as *Coniophanes, Drymobius, Leptodeira, Smilisca* and *Hypopacus*. However, among the reptiles and amphibians, as well as the mammals, the greatest reduction in tropical fauna is found in southern Tamaulipas (Martin, 1958).

DISCUSSION

Although our analysis in confined to eastern Mexico, some interesting comparisons can be made with the tropical biota of the Pacific Coast. Arid tropical vegetation and the genera *Macrotus, Balantiopteryx, Chilonycteris, Pteronotus, Mormoops, Glossophaga, Desmodus, Natalus, Rhogeesa* and *Nasua* extend far-

TABLE 2.—*Northern limits of neotropical mammals*

LOCALITY AND APPROX. ELEV.	REFERENCE	SPECIES PRESENT
San Luis Potosí:		
A. Tamazunchale, 120 m.	Dalquest, 1953	1. *Tamandua tetradactyla*
B. Xilitla and vicinity 630–1350 m.	Dalquest, 1953	2. *Sturnira ludovici*
		3. *Coendou mexicanum*
		4. *Cuniculus paca*
		5. *Potos flavus*
		6. *Galictis canaster*
C. Río Verde, 990 m.	Dalquest, 1953	7. *Molossus major*
D. Valles, 75 m.	Koopman, 1956	8. *Balantiopteryx plicata*
E. El Salto, 660 m.	Dalquest, 1953	9. *Carollia perspicillata*
Tamaulipas:		
F. Rancho del Cielo and vicinity, 1000–1320 m.	Goodwin, 1954 Hooper, 1953 present report	10. *Marmosa mexicana* 11. *Enchisthenes harti* 12. *Oryzomys alfaroi*
		13. *Reithrodontomys (Aporodon) mexicanus*
		14. *Mazama americana*
Pano Ayuctle, 100 m.	Goodwin, 1954 Hooper, 1953 de la Torre, 1954	15. *Micronycteris megalotis* 16. *Sturnira lilium* 17. *Artibeus jamaicensis*
		18. *A. lituratus*
		19. *A. cinereus*
		20. *Eira barbara*
G. 2 km. W of El Carrizo, 800 m.	Baker, 1951	21. *Philander opossum* 22. *Heterogeomys hispidus*
H. Jaumave, 730 m.	UMMZ specimens	23. *Macrotus mexicanus*
I. 10–16 mi. WSW Piedra, 400 m.	Anderson, 1956	24. *Chilonycteris parnellii* 25. *Glossophaga soricina*
		26. *Centurio senex*
		27. *Natalus mexicanus*
J. 2 mi. S Victoria, 400 m.	Davis, 1951	28. *Molossus rufus*
K. 30 km. NW Victoria, 1000 m.	Málaga-Alba, 1954	29. *Diphylla ecaudata*
L. La Pesca, 10 m.	Anderson, 1956	30. *Rhogeesa tumida*
M. Rancho Santa Rosa, 260 m.	Anderson, 1956	31. *Pteronotus davyi*
N. 8 mi. SW Padilla, 100 m.	Lawrence, 1947	32. *Oryzomys melanotis*
Nuevo León:		
O. 25 km. SW Linares, 700 m.	Málaga-Alba, 1954	32. *Desmodus rotundus*
P. 20 mi. NW General Teran, 300 m.	Hooper, 1947	33. *Oryzomys fulvescens*
Texas:		
Q. Hidalgo Co., 60 m.	Blair, 1952*b*	34. *Oryzomys couesi*
R. Raymondville, 30 m.	Blair, 1952*b*	35. *Liomys irroratus*

TABLE 2.—*Continued*

LOCALITY AND APPROX. ELEV.	REFERENCE	SPECIES PRESENT
Coahuila and West Texas:	Baker, 1956	36. *Choeronycteris mexicana*
	Miller and Kellogg, 1955	37. *Leptonycteris nivalis*
Edwards Plateau, Texas:	Blair, 1952*a*	38. *Mormoops megalophylla*
	Blair, 1952*b*	39. *Nasua narica*
Eastern United States:	Miller and Kellogg, 1955	40. *Dasypus novemcinctus*
		41. *Didelphis marsupialis*

ther north on the western side. On the other hand the humid tropical fauna and plant formations, e.g., Cloud Forest, Tropical Evergreen Forest and Rainforest, are absent or poorly represented on the Pacific slope north of Chiapas. As a general rule for those species or vicariant species occurring on both sides of Mexico, the arid tropical forms range farther north on the west, and the humid tropical forms farther north on the eastern side. This pattern is evident also in the distribution of lowland tropical birds, reptiles, insects, etc.

Other than noting a rather close "fit," it is beyond our purpose to explore the causal relationship between formation and fauna. In brief our conclusions may be summarized as follows:

1. The decline of the tropical fauna in eastern Mexico corresponds with the vegetation gradient.
2. Where the vegetation gradient steepens and a plant formation is lost, one finds a variety of tropical animals at their range limits.
3. In southern Tamaulipas the northern limit of many tropical mammals corresponds roughly to the boundary of Tropical Deciduous Forest. Contributing to the rich tropical fauna of the Gómez Farías region are relict outposts of Tropical Evergreen Forest and Cloud Forest.
4. The problem of establishing a Nearctic-Neotropical faunal boundary in eastern Mexico can be approached realistically in terms of steps in an environmental gradient.

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Query: Where is the best place to learn the phylogeny of *Paradolichotis*, the chorology of *Heliophobius*, or the location of the active sciurologist nearest to Punxsutawney? Answer, p. 56.

ECOLOGICAL OBSERVATIONS ON LASIURINE BATS IN THE NORTH BAY AREA OF CALIFORNIA

By Denny G. Constantine

During the period July 5 through September 16, 1954, while collecting bats for a bat rabies survey (Enright *et al.*, 1955), the writer conducted an extensive search for the roosting sites of lasiurine bats in Yolo, Napa, Lake, Sonoma and Marin counties, California. Native and domestic flora were investigated to the limit possible by one worker with ordinary bat-collecting equipment. A few observations were made that fall and the following spring. Successful experiences may be summarized as follows.

Lasiurus borealis teliotis, western red bat.—On August 9, 500 fig trees were closely inspected in an orchard at Esparto, Yolo County. One immature male red bat was found hanging on the outer side of a leaf, 5 feet above the ground, on the southwest side of a fig tree. The following day an adult female red bat, an immature female and an immature male were discovered at the cemetery at Capay, Yolo County, hanging in close apposition within a leafy overhang on the southern exposure of a China berry tree, at an elevation of 25 feet.

An adult male red bat was found August 12 in an apricot tree in Shell Orchard, 1 mi. S Rumsey, Yolo County, and the following day another adult male red bat was discovered in an apricot tree in Forest Orchard, 1.5 mi. S Rumsey.

The apricot trees of Belflower Orchard, 1 mi. S and 2 mi. W Esparto, were investigated August 26. An adult male red bat and an immature male were found hanging in separate trees, and a third red bat, which escaped capture, was found in another tree. A cluster of three red bats, hanging in still another tree, escaped by flying, and a group of approximately 15 red bats similarly dispersed when discovered. Thereafter, three adult females, three immature females and three immature males were captured as individuals in separate trees. No bats were found in nearby almond, orange or fig trees. Another adult male red bat was taken here in an apricot tree September 5. This orchard was investigated on three occasions during the following winter, when no bats were found.

A female red bat was captured while hanging in an overhang produced by the overlapping canopies of two fig trees at Black Winery, 2 mi. SE Cloverdale, Sonoma County, on September 8.

The Matsumoto Orchard, about 1 mi. S and 4 mi. W Esparto, was visited on March 27, 1955. The previous summer Mr. Matsumoto had related his bat experiences, gained during some 30 years of residence in the area. "In February or March reddish bats appear in the small orange grove just west of the house, selecting the south or southeast sides of trees. Later a somewhat larger and darker bat appears. The bats gradually move out of the orange trees into the nearby apricot trees, as the latter develop leaves. When handled or disturbed

the bats fly away but are back the next day. The bats fly more readily on warm days. No bats are present in winter." Presence on unspecified dates of bats in orange trees had been claimed by other orchard owners in the county, but the writer had found none in orange trees the previous summer and fall. On this date only a few leaves were present on nearby apricot trees, including Belflower Orchard, and no bats were found in apricot trees. Mr. Matsumoto stated that bats were now in the orange trees. The eleven orange trees were examined, and three large trees contained red bats. One tree contained two bats, one of which was captured and proved to be a male. The other flew when touched. Both bats were a dark red color, typical of males captured that day and less yellow than the female that was captured later. These two bats were on the south side of the tree, 3 feet apart, hanging at an elevation of 5½ feet. Another tree contained a female red bat, hanging on the south side of the tree, at an elevation of 8½ feet. The third tree contained three males, hanging 3 feet apart on the south, southeast and east sides of the tree at elevations of about 5 feet 8 inches. The air temperature was 70°F., and the sky was heavily overcast. Loud talking at a distance of one foot disturbed the bats only to the point of slight ear movement and slight opening of the eyes. However, they readily flew when handled. One bat, when realighting on a tree, was breathing rapidly, but it did not take wing again despite the disturbance of walking and talking persons.

The Matsumoto Orchard was again visited April 17, 1955. No bats were found in the orange trees, which were then blossoming and attracting many bees. An examination of 30 nearby apricot trees, now fairly heavily leafed, revealed no bats. Nearby Belflower Orchard was then visited, and 30 apricot trees were examined. One red bat was observed in a heavy clump of leaves, about 35 feet from the ground, on the very top of the tree. The bat was swinging back and forth, 45° from vertical on either side, as wind blew through the leaves. The sky was very cloudy, as it had rained an hour before. The air temperature was 62°F. The bat was left undisturbed.

An analysis of apricot trees where red bats were found, as contrasted with apricot trees where they were not found, suggests that in summer these bats select places with the following characteristics: the tree should be well-pruned and about 15 to 20 feet in height, possessing rigid branches and short stems, which provide minimum movement in wind. This type of tree has a single, well-defined, spreading canopy, and it lacks lower limbs or perches from which birds might conceivably discover bats. Branch angles are about 45°, presumably facilitating launching and alighting. The tree should contain dark, dense foliage. The general area should be warm and quiet with a multiplicity of similar but shorter trees, spaced 15 to 20 feet apart. Dark, usually recently plowed ground, providing little reflected light, was consistently present beneath the trees. Trees were usually growing on hillsides. Few or no birds were present.

Red bats in apricot trees were usually situated at about 8½ feet elevation, clinging to small branches or petioles, completely surrounded by leaves except

directly beneath, on the outward exposure of a limb. Bats apparently chose any side of a tree during summer, but that side provided adequate flight space, facing downhill, on a small clearing, or over shorter trees.

Red bats were discovered in summer at temperatures between 80° and 95°F., when they were quite active and capable of flight.

At 10:45 AM, March 22, 1955, while driving along a country road near Davis, Yolo County, the author noticed a California jay, *Aphelocoma californica*, pecking at an object at the side of the road. The object proved to be an adult female red bat, lying on its back with wings extended and curved upward. The auto was stopped and, as the site was approached, the jay flew away and a male Brewer's blackbird, *Euphagus cynocephalus*, alighted about 2 feet from the bat. When the writer arrived at the site the blackbird flew away. Leafless walnut trees, containing fairly dense growths of mistletoe, extended over the road at this point. The day was sunny and warm and no wind was evident. The bat lived several days in captivity, after which it was killed and prepared as a specimen. No obvious external or internal injuries were present. The eastern blue jay was earlier reported (Allan, 1947) attacking a red bat.

Lasiurus cinereus cinereus, hoary bat.—Preparations were made on August 17 to shoot bats at the edge of a pond on the Tevis Ranch, about 9 mi. NW Bolinas, Marin County. At dusk a fog bank moved through the forest and at its leading edge several bats were flying. An adult female hoary bat was shot at this time. While situated in a similar situation on the Kettenhofen Ranch, about 6 mi. S Olema, Marin County, on September 1, a fog bank was observed moving inland. Again, bats were present at the leading edge of the fog and another adult female hoary bat was shot.

An adult female hoary bat was discovered hanging to a small branch, 20 feet from the ground, in a leafy overhang produced by the overlapping canopies of two cherry trees in Brione Orchard, 3 mi. NW Bolinas, on September 1. The bat was on the west side of the trees over dark, recently turned earth. The following day an adult male hoary bat was found hanging 15 feet above plowed ground on the rigid, nearly upright limb on the north side of a cherry tree on the Martinelli Ranch, about 2 mi. NW Bolinas. In each place adequate flight space was present. Air temperatures were above 75°F., and the bats were quite active.

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DISPROPORTIONATE SEX RATIOS IN HIBERNATING BATS

By Wayne H. Davis

It is known that populations of bats hibernating in caves generally contain a preponderance of males. Griffin (1940) and Hitchcock (1950) in New England, Mohr (1945) in Pennsylvania, and Eisentraut (1947) in Germany have pointed this out. However, the reasons for these disproportionate sex ratios have never been determined. Possible explanations of this phenomenon have been advanced. However, there has been very little investigation of these theories. The present study, involving over 4,000 eastern pipistrelles, *Pipistrellus subflavus,* in the winter populations of 48 caves in West Virginia, is an attempt toward determining the cause of the preponderance of males in these hibernating populations.

There are three possible factors which could be responsible for the greater number of male bats found hibernating in caves: (1) more males than females are born; (2) the males have a higher rate of survival; or (3) many of the females spend the winter elsewhere. The first possibility seems hardly tenable. To my knowledge, no mammal is known in which a marked difference in the ratio of the sexes exists at the time of birth. Furthermore, it has been found that in the little brown bat, *Myotis lucifugus,* there are as many of one sex as the other at birth. Griffin (1940) found that a group of juveniles of this species in Massachusetts contained 440 females and 450 males, and Cagle and Cockrum (1943) found that a group of young in Illinois contained 213 females and 219 males. Rice (1957) found that 51 per cent of the 2,847 juvenile *Myotis austroriparius* which he examined in Florida were males. Pearson, Koford and Pearson (1952) found that of all the very young *Corynorhinus rafinesquii* which they examined, 128 were males and 126 females. Although no study has been made on the sex ratio of *Pipistrellus subflavus* at birth, it seems reasonable to assume that difference in sex ratios at birth can probably be ruled out as a factor contributing to the great preponderance of males among the hibernating populations of this species.

The second possibility, that of a differential survival rate of the sexes, seemed worthy of investigation. Two caves in West Virginia which contain large numbers of wintering pipistrelles were chosen for such a study. Nearly 400 pipistrelles were gathered and banded in each of these caves in the early spring of 1952. These populations were visited and the bats gathered and examined again in subsequent winters. Band numbers on those which had returned from the previous winter were recorded, and the nonbanded bats were tagged. Thus the population was divided roughly into different age groups. That is, as a group those banded in 1952 would be older than those banded in 1953, etc. The information thus obtained seems to show that the males in these populations have a higher rate of survival than do the females. Observations in Greenville Saltpeter Cave, Monroe County, West Virginia, in five different

years show that the over-all population consisted of 80, 80, 76, 82 and 72 per cent males. At the same time it was found that of those recovered after having lived two, three, four and five summers beyond the banding date, the proportion of males was 92, 89, 91 and 94 per cent, respectively. On the other hand, the nonbanded bats encountered on the second, third, fourth and fifth trips to this cave made up groups composed of 75, 71, 77 and 63 per cent males, respectively. These groups would be younger than the over-all population. Of the 320 males banded in the spring of 1952, we recovered 121, or 38 per cent, in the winter of 1953, whereas we were able to recover only 11, or 14 per cent, of the 78 females banded at that time. There is, of course, the possibility that the females among the older groups have a greater tendency to go elsewhere in winter than do the younger ones. Similar results with respect to comparative survival were obtained in the other cave studied (Table 1).

TABLE 1.—*Survival data on Pipistrellus subflavus gathered December 27–28, 1956*

	GREENVILLE SALTPETER CAVE			THORN MOUNTAIN CAVE		
	♂♂	♀♀	% ♂♂	♂♂	♀♀	% ♂♂
Total population handled	303	118	72	319	88	78
New bats banded	151	88	63	194	69	74
Returns from 1955	26	11	70	30	9	77
Returns from 1954	42	11	79	35	4	90
Returns from 1953	38	5	88	42	6	88
Returns from 1952	46	3	94	18	0	100

In the course of this study it was found that some pipistrelles remain in the caves in a torpid condition in the latter part of May and in June. These animals were all males. On May 20, 1951, 47 males and no females were found in one cave. The fact that some of the males tend to remain in the caves much longer in the spring than do the females, and thus are not exposed to the dangers of the outside world for as long a period of time, may account for some of the difference in the survival of the sexes.

If the difference in the rate of survival of the two sexes of this bat were the only factor concerned with the maintenance of the 4:1 ratio of males to females in the hibernating populations in West Virginia, then this ratio should hold among the summer breeding populations of the region, if these two represent the same populations. In order to investigate this, pipistrelles were shot in flight and the sex ratio was determined. Of the 134 adults shot outside the caves in West Virginia, only 53 per cent were males. Seven specimens in this sample were pregnant females taken in June. Since gravid females are more easily collected than males, the inclusion of these may bias the sample. If all pipistrelles taken during June are omitted for this reason, a sample of 111 remains, of which 55 per cent are males. This is a far different proportion of males than that found in the hibernating winter populations. Thus, there must be some

factor in addition to a differential survival rate which contributes to the maintenance of the sex ratio in the latter populations.

The third and last alternative which may be influential in causing the unequal sex ratio is the possibility that many of the females may winter elsewhere. An attempt has been made to investigate this possibility. Perhaps more females spend the winter in caves farther south. The sex ratios in these caves would then be different from those of West Virginia. Several caves in Missouri were examined and it was found that of 431 pipistrelles handled during the winter months, 307, or 71 per cent, were males. Again, in a population of 281 of these bats in a cave in northeastern Alabama, 71 per cent were males. Still farther south, in extreme southwestern Georgia, a cave was investigated on February 4, 1955. It was found to contain 479 pipistrelles. Of these, 235 were males and 244 females, or 49 per cent males. Thus it can be seen that the preponderance of males decreases from north to south: 91 per cent males in Ontario and Quebec (Hitchcock, 1950), 80 per cent in West Virginia, 71 per cent in Missouri and northern Alabama, and 49 per cent in southern Georgia.

As evidenced by their numbers in summer, the pipistrelle is a much more abundant bat than the hibernating populations in the caves and mines would indicate. Many of them must winter elsewhere. Also, there must be a preponderance of females among those wintering outside the caves, for the sex ratio in summer is far different from that in most caves in winter.

The percentage of males in the over-all population in the two caves studied in West Virginia was found to be different in different years. For example, in Greenville Saltpeter Cave (with samples of over 400 bats) it was found that 82 per cent were males in December, 1955, and 72 per cent males in December, 1956. In order to test the significance of these differences, a chi-square test was used. The five-year averages for each cave were taken as the expected value, to be compared with the data from each year. The two-by-two-by-five table was found to be homogeneous, showing that the fluctuations from year to year are alike in the two caves. Thus, we can add the data from the two caves together, keeping years and sexes separate. Upon studying the results obtained, it is seen that there was more difference in the year-to-year sex ratio than could be ascribed to random sampling. Further, it appears that there was a difference in the sex ratio of the last year as compared to the first four. Thus, there must have been some factor in 1956 which significantly altered the sex ratio in these caves. In one cave there was a drop from 82 to 72 per cent males, while a corresponding drop from 85 to 78 occurred in the other cave.

Since the sex ratios among hibernating winter populations differ clinally from north to south, it seems likely that the yearly changes in sex ratio within a population can also be correlated with climatic differences. In this respect it is interesting to find that climatically the year 1956 was considerably different from the 75-year average for West Virginia. The winter was unusually mild, with fair weather prevailing until late November. Temperatures in

December averaged 8° above normal and general cold weather did not set in until late December.

The winter climate of a region seems to be the most important factor controlling the sex ratios in hibernating cave populations of pipistrelles. The harsher the winter, the higher is the percentage of males wintering in the caves. In Thorn Mountain Cave, Pendleton County, West Virginia, pipistrelles were not nearly so common on December 28, 1956, as they had been in previous winters. It is quite likely that many of those which usually winter in this cave had not yet arrived. Sealander (*in litt.*) has noticed that during mild winters there are not nearly so many pipistrelles in the caves in northwestern Arkansas as during cold winters. That they may winter outside the caves in these regions is not unlikely, for it has been shown by Davis and Lidicker (1956) that the red bat, *Lasiurus borealis*, which is not a cave-dwelling species, regularly winters in the Ohio River Valley.

SUMMARY

It is established that 80 per cent of the population of *Pipisterellus subflavus* which hibernates in the caves of West Virginia are males. The males among this population have a higher rate of survival than the females. The high preponderance of males in this population cannot be due to this factor alone, however, for the summer population has an entirely different sex ratio. The tendency for the males to remain in the caves in an inactive state in summer may explain part of the discrepancy, and may also be responsible for part of the difference in survival. The percentage of females hibernating in caves increases as one goes southward. In a cave in southern Georgia the sexes were about equal. The sex ratio of a hibernating population changes somewhat from year to year. This seems to be due to differential responses of the sexes in *Pipistrellus subflavus* to yearly climatic fluctuations.

The disproportionate sex ratios among hibernating populations of pipistrelles seem to be due to a combination of two factors: a difference in survival rate of the sexes, and the probable wintering of large numbers of females outside the caves.

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MEIBOMIAN GLANDS IN *LAGURUS*

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These sebaceous-type glands are located in the tarsal plate of the upper and lower eyelids of all mammals. Although anatomists have long been aware of these glands, their taxonomic significance has been only recently recognized (Sulc, 1929). Following an extensive study of tarsal glands in microtine rodents, Quay (1954*a*) ascertained that "variations in Meibomian gland number cannot be correlated with sex, season, or age" and "the number of Meibomian glands present and their morphology and location are species characteristics." In his comprehensive study of the Meibomian glands in the subfamily Microtinae, Quay (*op. cit.*) concluded that the gland number and their morphology in most instances parallels the currently accepted phylogeny of this subfamily. That is, in the more primitive genera and species the glands are of more uniform size and occur in greater numbers than in the more advanced representatives of this subfamily.

According to Quay (*op. cit.*), the number and morphology of the tarsal glands in animals of the genus *Lagurus* would indicate that these voles are among the more advanced, if not the most advanced, representatives of the subfamily Microtinae. It should be noted, however, that this supposition was based upon examination of the eyelids of three specimens of [?] *Lagurus pauperrimus* from the University of Michigan Museum of Zoology. The skulls, preserved bodies and slides of the Meibomian glands of these animals (Nos. 78505, 78506 and 78507) have been loaned to me by Drs. William H. Burt and W. B. Quay. Because these specimens had been misidentified, the conclusions of Quay (1954*a*) relative to the phylogenetic position of the genus *Lagurus* are untenable.

Materials and methods.—In the course of this study, 60 whole mounts of Meibomian glands have been examined. These whole mounts were obtained from representative members of the genus *Lagurus* as follows: *L. lagurus*, 7; *L. curtatus pallidus*, 16; *L. c. levidensis*, 7; *L. c. orbitus*, 5; *L. c. intermedius*, 6; *L. c. curtatus*, 9; *L. c. pauperrimus*, 10. Whole mounts of Meibomian glands were prepared following the method of Quay (1954*b*). Illustrations of the tarsal glands were made with the aid of the camera lucida.

Description of Meibomian glands.—Meibomian glands in both upper and lower eyelids extend almost continuously from the lacrimal caruncle anteriorly to and including the extrapalpebral gland posteriorly. The lacrimal caruncle is a small mound of skin bearing a tuft of hairs which, contrary to Quay (1954*a*), point anteriorly. The duct of the exorbital lacrimal gland separates the tarsal glands of the upper and lower eyelids posteriorly.

In animals of *L. lagurus*, the Meibomian glands (Fig. 1A) are markedly palmate on both upper and lower eyelids. The duct system for each gland seems to be much more diffuse than are the ducts of these glands in the North American representatives of this genus. The glandular tissue is, in most cases,

distinctly removed from the proximal part of the duct. Extrapalpebral glands are distinct not only in size differential between upper and lower eyelids, but also by virtue of the vertical arrangement of these glands in the upper eyelid. The upper extrapalpebral glands seem to be glandular extensions of the upper tarsal glands, with each gland having a separate duct opening into the duct of the exorbital lacrimal gland. In contrast, the lower extrapalpebral gland is small and has only a single duct which empties into the posterior corner of the lower eyelid. (For tabulation of gland number, see Table 1.)

The Meibomian glands in animals of *L. curtatus* can readily be distinguished from those of *L. lagurus* by means of the diagnostically different extrapalpebral glands. In the former species, the extrapalpebral glands do not open by separate ducts into the duct of the exorbital lacrimal gland, but rather by a single duct which empties either into the posterior corner of the eyelids or into the distal end of the duct of the exorbital lacrimal gland. In addition, the tarsal glands in animals of *L. curtatus* are less palmate and the glandular tissue is more extensive toward the inner margin of the eyelids than in *L. lagurus*. Further, there seems to be a slight to a marked tendency for the anterior glands to overlap

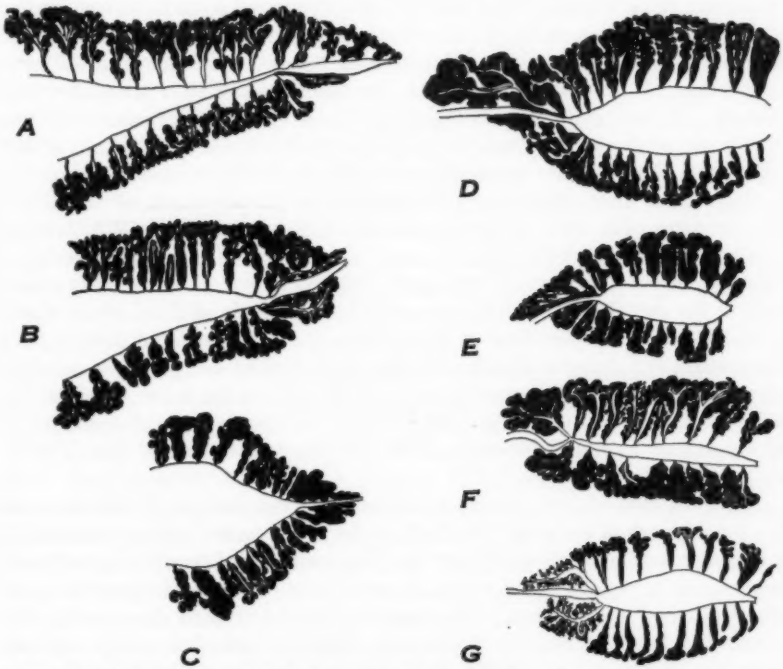

FIG. 1.—Meibomian glands in *L. lagurus* and the subspecies of *L. curtatus*. A, *L. lagurus*; B, *L. c. curtatus*; C, *L. c. intermedius*; D, *L. c. pauperrimus*; E, *L. c. levidensis*; F, *L. c. orbitus*; G, *L. c. pallidus*.

TABLE 1.—*The number of Meibomian glands in the species and subspecies of the genus Lagurus*[*]

	DORSAL EYELID			VENTRAL EYELID			BOTH EYELIDS		
	N	$\bar{x}$	*R*	*N*	$\bar{x}$	*R*	*N*	$\bar{x}$	*R*
L. lagurus	6	11.83	10–13	6	11.5	10–13	6	23.33	21–26
L. c. pallidus	12	12.0	10–14	12	10.0	8–12	12	21.91	18–25
L. c. pauperrimus	6	11.33	10–15	5	10.4	9–11	5	21.70	20–25
L. c. curtatus	6	11.33	10–13	6	11.2	10–12	6	22.5	21–25
L. c. intermedius	6	11.20	11–12	6	10.16	10–11	6	21.3	21–23
L. c. levidensis	7	9.83	8–11	7	8.17	6–11	7	18.0	14–21
L. c. orbitus	5	10.65	10–11	5	9.55	9–10	5	20.0	20

[*]In the table, *N* = number of specimens examined, $\bar{x}$ = the mean gland number, *R* = observed range in gland number.

the distal tips of the posterior adjacent glands.

Within the subspecies of *L. curtatus*, the morphology of the tarsal glands shows considerable variation. In animals of *L. c. pallidus* (Fig. 1*G*) the tall filiform condition of both the upper and lower tarsal glands is distinctive. Moreover, the lobules of which each gland is composed seem to be smaller and more abundant than in the glands of the other subspecies. Tarsal glands in animals of *L. c. levidensis* (Fig. 1*E*) are characterized by the lack of the filiform-type gland. In the latter subspecies, the Meibomian glands are quite wide distally and proximally on both upper and lower eyelids. This latter condition is also seen in the tarsal glands on the lower eyelids in animals of *L. c. orbitus* (Fig. 1*F*). The palmate condition of the tarsal glands, as seen in animals of *L. lagurus*, is most closely approximated in the tarsal glands of animals of *L. c. curtatus* (Fig. 1*B*). In general, the tarsal glands in animals of *L. c. intermedius* (Fig. 1*C*) lack the palmate condition. The tarsal glands of these latter animals are broad, compactly arranged, with the largest glands usually occurring in the middle. The Meibomian glands in animals of *L. c. pauperrimus* (Fig. 1*D*) are best identified by the pronounced overlap of the distal tips of the middle and anterior glands over the distal tips of the posterior adjacent glands. While this latter aspect is occasionally seen in the tarsal glands of the other subspecies of this species, the extent of overlap is never as extensive as in animals of *L. c. pauperrimus*. (For tabulation of the tarsal glands of *L. curtatus*, see Table 1.)

Statistical analysis.—To ascertain whether the morphological differences in the tarsal glands of the species and subspecies of the genus *Lagurus* were valid, it was deemed advisable to subject the total tarsal gland number to statistical analysis. It is worthy of note that, in analysis of variance of the total tarsal gland number, a significant difference is obtained at both the specific and subspecific levels. Since the Meibomian glands are morphologically and statistically distinct at the specific level, whereas the tarsal glands in the subspecies of *L. curtatus* show less morphological distinction, it is toward this latter group that statistical analysis of variance will be directed.

In the analysis of variance chart that follows, Tukey's test of least significance (*Ts*) has been employed to ascertain the significant difference between the means of any two of the populations analyzed. In the following equations, "*q*" is the range of *K* treatments divided by the standard deviation of the treatments. K_o is the number of observations in a group, εK is the sum of the individuals, εK^2 is the sum of the squares of *K* treatments, and S^2 is the mean square of individuals.

TABLE 2.—*Analysis of variance of the total tarsal gland number in the subspecies of L. curtatus*

	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE
Groups	5	91.58	18.31
Individuals	35	114.42	3.269

$$F = \frac{18.31}{3.26} = 5.601 \qquad F = \left[\begin{matrix} 5 \\ 35 \end{matrix} \; 0.01 \right] = 3.60$$

From Table 2, it is apparent that the *F* value is significant, thus indicating more than one population. In addition, Tukey's test of least significance indicates that animals of *L. c. levidensis* are significantly different from those of *L. c. pallidus, L. c. pauperrimus* and *L. c. curtatus* at the 1 per cent level. Moreover, by means of this same test, animals of *L. c. levidensis* are significantly different at the 5 per cent level from all subspecies of *L. curtatus* with the exception of *L. c. orbitus*. This apparent close relationship between *L. c. levidensis* and *L. c. orbitus* has been noted previously (Dearden and Lee, 1955) and by this author in comparative studies of the baculum (Dearden, 1958).

Discussion.—In his comprehensive study of the Meibomian glands, Quay (1954*a*) ascertained that the most primitive Microtinae (lemmings) have the least gland reduction, whereas the more advanced Microtinae (voles) are characterized by a slight to a pronounced gland reduction. If this is true, and I believe it is, then animals of the genus *Lagurus* are not among the more advanced voles, as indicated by Quay (1954*a*), but rather closely associated with the more primitive Microtini and with the more advanced Lemmini.

From Table 1 it can be readily ascertained that not only the average total tarsal gland number, but also the average gland number of the upper and lower eyelids, indicates that the representatives of this genus are phylogenetically more primitive than heretofore considered. If the average total tarsal gland number as well as the averages of the dorsal and ventral tarsal glands are compared with the corresponding averages of Meibomian glands in microtine rodents, as ascertained by Quay (1954*a*), it is readily ascertained that the affinities of these mammals lie with the Lemmini. The most closely related genus of the Microtini, according to this study, is the genus *Clethrionomys*.

When the morphological and statistical analyses of the Meibomian glands of the subspecies of *L. curtatus* are considered as corroborative evidence, it

TABLE 3.—*Total tarsal glands*

SUBSPECIES OF *L. curtatus*	MEAN	STANDARD ERROR
L. c. pallidus	21.91	$\sqrt{\frac{3.26}{12}} = 0.522$
L. c. pauperrimus	21.60	$\sqrt{\frac{3.26}{5}} = 0.808$
L. c. curtatus	22.50	$\sqrt{\frac{3.26}{6}} = 0.737$
L. c. intermedius	21.30	$\sqrt{\frac{3.26}{6}} = 0.737$
L. c. levidensis	18.00	$\sqrt{\frac{3.26}{7}} = 0.682$
L. c. orbitus	20.20	$\sqrt{\frac{3.26}{5}} = 0.808$

$$K_o = \frac{1}{N-1}\left(\varepsilon K - \frac{\varepsilon K^2}{\varepsilon K}\right)$$

$$K_o = \frac{1}{5}\left(41 - \frac{315}{41}\right)$$

$$K_o = 6.66$$

$$Ts = q\sqrt{\frac{S^2}{K_o}}$$

$$Ts = 5.17\sqrt{\frac{3.26}{6.66}}$$

$$Ts = 3.61 \text{ at 1 per cent}$$

$$Ts = 2.98 \text{ at 5 per cent}$$

appears that a rather definite trend toward species designation is in progress for these subspecies. Of these subspecies, with regard to the tarsal glands, animals of *L. c. levidensis* seem to warrant specific designation. If additional morphological and distributional data offer corroborative evidence, it seems reasonable to assume that this population constitutes a valid species, with animals of *L. c. orbitus* being a subspecies of this species.

Davis (1939: 325) considered the North American representatives of the genus *Lagurus* to be morphologically distinct enough to warrant generic designation. Accordingly, Davis (*loc. cit.*), using the subgeneric designation pro-

posed by Thomas (1912: 401), raised the subgenus *Lemmiscus* to full generic status. Subsequent workers have been somewhat vacillatory in their acceptance of these voles at the generic rank. While Meibomian gland studies in voles of the genus *Lagurus* are quite diagnostic at the specific level, somewhat less diagnostic subspecifically, there seems to be no valid justification from these studies that would warrant generic consideration for the North American representatives of this genus.

Summary and conclusions.—In this study, 60 whole mounts of Meibomian glands representing two species of the genus *Lagurus* have been described and the North American forms have been statistically analyzed at the subspecific level.

The important conclusions derived from this investigation are as follows:

1. The phylogenetic position of the genus *Lagurus* is much more primitive than heretofore considered.

2. If the reduction in Meibomian gland number parallels in most instances the currently accepted phylogeny of the subfamily Microtinae, then the proper phylogenetic position of the genus *Lagurus* is as follows:

Subfamily Microtinae
Dicrostonyx
Synaptomys
Lemmus
Lagurus
Clethrionomys

3. From statistical and morphological analysis of the tarsal glands, animals of *L. c. levidensis* seem to warrant consideration as a full species.

4. Comparative studies of the Meibomian glands of animals of *L. lagurus* and of *L. curtatus* do not lend credence to the generic status afforded the North American representatives of this genus.

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THE COLUMBIAN GROUND SQUIRREL IN NORTHWESTERN MONTANA

By Richard H. Manville

Among the many forms of ground squirrels inhabiting western North America, the Columbian ground squirrel, *Citellus columbianus* Ord, occupies a large range from the higher grassy plateaus and sagebrush plains of eastern Washington and Oregon to elevations well up in the mountains of western Montana, and northward several hundred miles into British Columbia and Alberta (Fig. 1). In agricultural districts it has done much damage to crops, particularly wheat and alfalfa, and it has also been involved as a reservoir of spotted fever and bubonic plague. Investigations of its life history and control, years ago, centered in the agricultural belt of eastern Washington and were well summarized by Shaw (1925*a–e*). But the animal's habits and significance differ markedly in the mountains to the east, where it is abundant and serves an important role in the ecology of the community. Bailey (1918) reported his widespread observations on this squirrel in Glacier National Park; knowledge of the species in the same area has been summarized in popular style by Lechleitner (1955). This also is the site of my observations, reported herein.

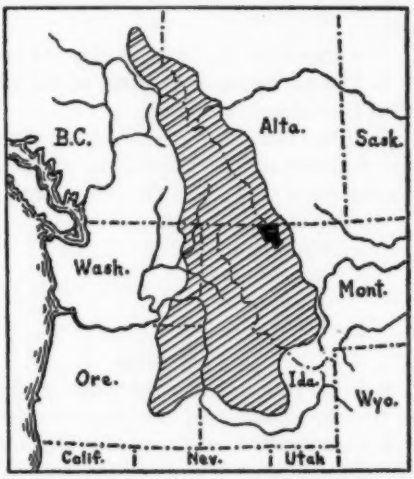

Fig. 1.—Approximate range of *Citellus columbianus* in western North America. The dark central area marks the location of Glacier National Park.

Area of observations.—This mountainous area of over 1,500 square miles, comprising parts of Flathead and Glacier counties in northwestern Montana and abutting on the Canadian boundary, was set aside as Glacier National Park in 1910. Its mountains rise abruptly from the prairies to the east and the Continental Divide runs its irregular course north and south through the Park. The lowest elevation, 3,050 feet above sea level, is at the western boundary; ten peaks rise above 10,000 feet. Timberline ranges from 7,000 to 8,000 feet. Most of the Park is in the heavily forested Canadian life zone; bits of Transition zone penetrate the Park on its eastern and western borders, and Hudsonian and Alpine communities occupy the higher levels. The climate is rigorous, with heavier precipitation, higher average temperatures and less severe winds on the western slopes; here the forests are more dense and the winters somewhat milder. At the higher elevations snow may fall in any month of the year; on the

eastern slopes 480 inches fell during the winter of 1953–54. A number of small mountain glaciers clothe the upper slopes. The climate at the lower eastern edge of the Park (at Babb, 4,500 feet) may be summarized as follows, after Maughan (1941): average January temperature, 17.7°; average July temperature, 60.1°; maximum, 96°; minimum, –53°F.; average growing season, 102 days, May 29 to September 8; average annual precipitation, 19.43 inches.

Methods.—Approximately five months were spent in the field, from June 22 to September 7, 1954, and from June 18 to September 1, 1955. Daily observations were made of squirrels at the Many Glacier Ranger Station; some of these became quite tame and it was possible to identify individuals, though none were trapped or marked. Widely scattered observations were made elsewhere as opportunity permitted, at low and high levels. Grinnell Glacier and Iceberg Lake were each visited at least once per week. In 1955, notes were made at Piegan Pass on August 5 and at Swiftcurrent Pass on July 30 and August 14. The Sperry Glacier area was visited on August 18–19, 1954, the Ptarmigan Wall on August 3, 1954 and August 9, 1955, and also the Belly River Valley on the latter date. A plot was laid out in meadowland near the shore of Sherburne Lake and five days were spent here mapping the workings, partially excavating the burrows and tallying the plants.

Description.—This species was first collected, in north-central Idaho, by the Lewis and Clark expedition of 1804–06; it was formally described by Ord in 1815. Two races of *Citellus columbianus* are now recognized, of which the typical form occurs throughout most of the range, including Glacier National Park. The other, *C. c. ruficaudus,* occupies northeastern Oregon and extreme southern Washington. The most nearly related form appears to be *C. parryi* (= *Spermophilus undulatus*) and its races of further north (Howell, 1938). The present form is among the largest of the ground squirrels; plump adults commonly weigh 14 to 18 ounces (Bailey recorded an old male of 24 ounces). The body is robust; the legs, tail and ears short; the tail moderately bushy (Plate I). Total length of adults is 10 to 16 inches and tail length 3 to 5 inches. The animals are protectively colored, blending well with their background. The upperparts are a mottled gray or grayish-brown; the legs, feet and underparts dark fulvous or tawny; the grayish tail may have a white tinge dorsally; the front of the head, from nose to ears, is a bright reddish-brown, whence the name of "red-noses" applied by the local Indians; a white ring surrounds the eye. There seems to be but a single annual molt, in June or July. The forefeet are well adapted for digging, with claws much larger than those of the hind feet.

Habits.—The Columbian ground squirrel, sometimes mistakenly called a "gopher" or, more frequently, "picket pin" by the farmers to the east, is generally a wary and suspicious creature. It is gregarious in habits, but less so than the prairie dog. Constantly alert, it warns other members of the colony when an enemy approaches, and promptly scurries to the nearest burrow, no matter to whom it may belong. Its sense of hearing is acute but it also relies heavily on sight for the detection of danger.

On coming forth from its burrow, first just the rufous nose and the eyes appear; after several seconds the shoulders are raised; still another pause, and it emerges completely and almost immediately sits up, with shoulders hunched, for perhaps ten seconds. If all seems safe, it then sits up erect, its nose twitching and arms held close to its breast in the alert "picket pin" position (Plate I). As it sits, it gives frequent twitches of its hindquarters, with the effect of a bobbing sandpiper. Only after a minute or more of this reconnaissance does it drop down to get food. This it eats while sitting on its haunches, slightly humped over, the food held securely in the forefeet (Plate I). For only brief periods, when apparently feeling perfectly secure, does it drop down to rest on all four feet.

The normal gait of the squirrel is a bounding series of leaps or a quick dash—it seems always in a hurry. Sometimes, when not alarmed, it *walks* slowly, one foot at a time, the entire body kept close to the ground. Almost invariably, when assuming the erect "lookout" pose, it flicks the tail vigorously two or three times. This may serve as a silent signal to other squirrels, as a distraction to possible predators, or simply as an expression of the animal's high-strung temperament.

Strictly diurnal in habits, the squirrel wastes no time during the summer months. I have seen it active at 5:30 AM in mid-July, and until dusk. In clear weather it may be abroad most of the day and even inclement weather does not always lessen its activity. Several times I have seen it foraging during light rain; on July 2, 1955, it was out off and on all day, during intermittent rain and snow, at temperatures between 35° and 40°F.

Although primarily a ground dweller, it does often sit on logs or rocks to watch for danger. On one occasion, near Ptarmigan Falls, I watched a ground squirrel climb, with some assurance, to the tip of a dead snag where it sat erect on its haunches, surveying the scene. The log, situated on a steep hillside, was free of bark and limbs and projected out 8 feet at an angle of 45° from the horizontal. The squirrel remained here for two minutes, not calling, but flicking its tail briskly when I whistled. At times these squirrels may climb into the lower branches of shrubs, seeking berries. Several made their way, quite clumsily, up a small lodgepole pine to a bird-feeding platform 6 feet high near our cabin.

It has been said that these squirrels seldom drink and they probably obtain much of their required water from moist vegetation or succulent foods. Snow is consumed at times, and once I observed two juveniles slowly and deliberately having a hearty drink from a melting snowbank. Their need for water is indicated by their local distribution, usually not far removed from some watercourse, however small. They probably do not voluntarily enter water, but they are capable of swimming. Walter Chance reported seeing one well-grown squirrel swimming in Swiftcurrent Lake, 100 yards or more from shore; how or why it got there remains a mystery. It was presumably swamped by the wash from a passing launch, and later drowned.

PLATE I

Characteristic poses of the Columbian ground squirrel. *A*, adult (left) and juvenile near Grinnell Glacier, 24 August 1955; *B*, adult near Iceberg Lake, 14 July 1955; *C* and *D*, juveniles, same occasion as *A*; *E*, adult near Many Glacier Ranger Station, 28 June 1955–less than one-third of the mound of excavated earth appears in the picture.

PLATE II

ABOVE: The Swiftcurrent Valley from the summit of Swiftcurrent Mountain; Altyn Peak at the left, Grinnell Point at the right, Sherburne Lake in the distance and the Many Glacier Ranger Station in the center of the picture. Columbian ground squirrels occur at the highest and lowest points shown. 14 August 1955.

BELOW: View eastward from meadows at Logan Pass; Piegan Mountain at left, Mount Reynolds at right, Red Eagle and Little Chief Mountains in distance. 29 July 1954.

Like all squirrels, these are afflicted with ectoparasites. They frequently pause to scratch and, late in the summer particularly, may be seen dusting themselves. They sprawl out on their bellies, limbs outstretched, and wriggle back and forth repeatedly in a seeming effort to work the dust into their pelage. On August 24, near the Grinnell Glacier, several juveniles were dusting energetically; a depression more than an inch deep had been worn in the dry soil beneath a low alpine fir by this activity.

Voice.—This is a highly vocal squirrel and, near a colony, its calls may be heard throughout the day. The note is a clear, sharp *chirp*, usually repeated three or four times, and may be heard for several hundred yards. It is customarily uttered while the squirrel is sitting erect; the mouth is opened wide and the abdomen forcibly contracted as the note is delivered, often accompanied by a flick of the tail. The notes differ in frequency and intensity under varying conditions, from the loud initial call of alarm, repeated at intervals of several seconds, to the soft, low *churr* of the mother as she gathers her brood at a burrow entrance or her quick, shrill note as she sends them underground. When not unduly alarmed, but retreating into its burrow to be on the safe side, a squirrel may emit a low, musical trill. When a group is approached by a potential enemy, the first squirrel to apprehend the threat utters a loud call of alarm; this is passed on in turn by others far and wide. If the danger continues, the cries become louder and faster until the squirrel bolts down a burrow, its notes blended in a final, twittering shriek. More distant squirrels continue the alarm with renewed vigor. The young when only a few hours old, are said to give a note similar to that of tiny kittens; old squirrels may also utter a "vibrating lip or tooth-grinding sound when excited" (Shaw, 1925*a*). I have heard neither of these sounds. The call notes attract attention to the squirrels when they might sometimes be overlooked. But not always are they used—on a number of occasions squirrels have dashed hurriedly to shelter without any sound audible to me. I gained the impression that they regarded themselves as not yet observed.

Habitat.—These squirrels are creatures of the open country or edges of forests and may be expected in almost any meadow, open slope or area cleared by fire or avalanche. Treeless or half-forested areas, flat meadows or rocky hillsides all come within their province (Plate II). In Idaho, Davis (1939) found them "along streams where the forest is open; never have I found them far from water or in heavily forested areas. Altitudinally they occur from about 700 feet at Lewiston up to over 8,000 feet in the Salmon River Mountains." Their burrows may be in the open, unprotected, on flat or steeply sloping ground, or may be located beneath boulders, logs or stumps. In mountain meadows many runways through the grass radiate out from a central den or connect various burrow systems. Near hotels and chalets in the Park they often live beneath buildings. Zonally, these squirrels are most prevalent in the Hudsonian but they also occur commonly in the lower Canadian Zone in open spots.

Apparently the situation differs considerably in the nearby region of Kootenai County, northern Idaho. Rust (1946) reported that the species, held in check by the many raptors and coyotes, was formerly a resident chiefly of the lower elevations in the Transition zone. "With the almost total extermination of many of the hawks and the greatly reduced number of predatory animals," accompanying the establishment of settlements in northern Idaho, the Columbian ground squirrel became abundant and "has been following up the more open sunny slopes and ridges and extending its range well into the Canadian zone and even to the border of the Hudsonian zone at elevations from 4,500 to 6,500 feet."

Home site.—A meadow occupied by ground squirrels, near the western end of Sherburne Lake, was selected as representative of the species' habitat at the lower levels (4,800 feet). The area was uncultivated but occasionally served as pasturage for horses. This spot was 0.9 mile east of the Swiftcurrent Lake (formerly McDermott Lake) dam, 200 yards south of the road to the Many Glacier area, and just west of the creek flowing from the Appekunny Basin. On July 12, 1955, a quadrat 40 feet square was staked out on level ground and marked with lines (Fig. 2). On four subsequent days, the last one August 16, this quadrat was examined in more detail.

The quadrat was well covered with sod and mixed vegetation. About a foot of humus and dark topsoil, mixed with stones and pebbles, comprised the upper layer of soil; beneath this was a band of clay, 2 to 3 inches thick, and further down a mixture of sand, rocks and gravel. Two sizable clumps of shrubs (prairie rose and shrubby cinquefoil) grew on slight prominences, possibly mounds from ground squirrel excavations of previous years. Elsewhere grew many grasses, a few small clumps of shrubs, and a variety of flowering plants. The following plants, listed in accordance with Standley (1921), were present on the quadrat:

Porcupine grass, *Stipa richardsonii*
Common timothy, *Phleum pratense*
Bear grass, *Xerophyllum tenax*
Star Solomon's seal, *Vagnera stellata*
Blue-eyed grass, *Sisyrinchium mucronatum*
Umbrella plant, *Eriogonum subalpinum*
Common western anemone, *Anemone globosa*
Yellow stonecrop, *Sedum stenopetalum*
Shrubby cinquefoil, *Potentilla fruticosa*
Cut-leaf cinquefoil, *Potentilla blaschkeana*
Showy cinquefoil, *Potentilla filipes*
Pale strawberry, *Fragaria glauca*
Old-man's-whiskers, *Sieversia ciliata*
Prairie rose, *Rosa bourgeauiana*
Silky lupine, *Lupinus sericeus*
Hairy locoweed, *Oxytropis splendens*
Wild geranium, *Geranium viscosissimum*
Evening primrose, *Oenothera strigosa*
Bearberry, *Arctostaphylos uva-ursi*
Jacob's ladder, *Polemonium parvifolium*
Silky phacelia, *Phacelia sericea*
American mint, *Mentha canadensis*
Horsemint, *Monarda menthaefolia*
Yellow beardtongue, *Pentstemon confertus*
Baby's-breath, *Galium boreale*
Pussytoes, *Antennaria arida*
Goldenrod, *Solidago missouriensis*
Golden aster, *Chrysopsis villosa*
Western yarrow, *Achillea lanulosa*
Balsamroot, *Balsamorrhiza sagittata*
Brown-eyed Susan, *Gaillardia aristata*
Ragwort, *Senecio pseudaurens*

On July 12 at least six ground squirrels, all yearlings or older, were present in the general area, but only one appeared to reside within the quadrat. By

July 26 the young of the year, in surrounding areas, were nearly full grown and one adult was still present on the quadrat. Little activity was noted on August 16, only one ground squirrel being seen. On this date the area was very dry; there had been no rain for the preceding 17 days. Probably the squirrels were already beginning to go into their period of dormancy.

A number of burrow entrances were well concealed in the shrubbery on the area, but many were also in the open with no attempt at concealment. One burrow about 15 feet long (*A–B*), which proved not to be connected with the rest of the system, was excavated on July 12; a week later it had been partly filled in and a few new burrows constructed. Most burrows that were no longer used were plugged with soil at the entrance. The typical burrow led down at an angle of about 45° and leveled off into the passages, quite consistently,

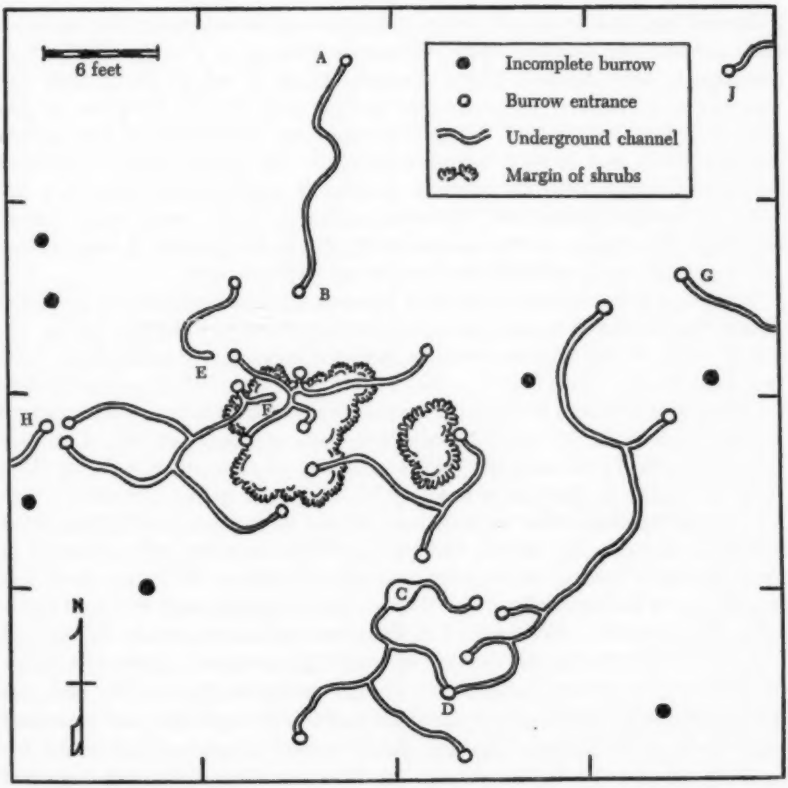

FIG. 2.—Plan of colony site on quadrat near Sherburne Lake (4,800 feet) partially excavated in July and August, 1955. For explanation of letters, see text.

at 11 to 12 inches below the ground surface; in a few instances, notably beneath the clumps of shrubs, these channels were as deep as 18 inches. There were no conspicuous new mounds on the area and soil from new excavations must have been either dispersed over the ground or redistributed in the underground channels. No new workings were observed after July 19 on the quadrat. One nest chamber (*C*), nearly 2 feet in diameter, was located on the quadrat; on August 16 it was well filled with a mass of cottony fibers, the fruit of *Anemone globosa*. No other underground chambers were found in the burrows excavated. Nor were any provisions noted for drainage of the burrows, although they are reported to be common, especially near the underground chambers, except in systems located on steep slopes.

Examination of the map of the quadrat (Fig. 2) reveals several noteworthy features which may or may not be typical. In only one case (*D*) did more than one channel lead directly from an entrance burrow; in only two cases (*E, F*) did a channel lead to a dead-end. Seven small burrows on the quadrat led nowhere and may have represented either exploratory diggings or abandoned efforts at constructing new channels. Three channels (*G, H, J*) led off the quadrat and were not traced further. Located on the quadrat were five major systems, closely associated but unconnected. There is a suggestion that several of the systems near the shrubs may, in time, become connected. The various junctions between different channels have no common pattern; it would appear that they are achieved by the expedient of tunnelling uniformly at the same level. Rather obviously, the systems on the quadrat were still in the process of construction and expansion, as is probably the case in any active colony.

In contrast to the extensive system of burrows at lower elevations, as described above, it is of interest to note the equivalent structures at the upper levels. On July 27, 1917, Bailey excavated and mapped a winter den at an altitude of 7,000 feet near Piegan Pass (Fig. 3). This system was occupied by a "moderately fat old female that was evidently preparing her winter quarters," and appeared to have been in use for several years. The more compact network of tunnels probably reflected not only the greater difficulty of excavating in the shallow, rocky soil, but also the shorter time available for such work. The system contained three openings—the main entrance with a large mound containing about 4 bushels of earth and stones, and two auxiliary openings half concealed in grass, probably serving as secondary avenues of escape. The main shaft was usually 3 or 4 inches in diameter. Nearly 8 feet from the main entrance was a large nest chamber, about a foot in diameter and a foot below the ground surface, well filled with the soft flat leaves of "glacier grass" (*Juncoides parviflorum*), a rush growing abundantly on the mountain slopes. The nest was damp and moldy at the base but the upper half was dry and clean and contained some fresh, green blades. This had plainly served as winter quarters for the squirrel and as a nest for her young. An older and deeper chamber contained the rotten remains of an old nest and a considerable quantity of excrement. Other chambers, near forks in the tunnels, may have served as storage sites

for excavated earth or as retreats from which to watch for invaders from either direction.

Social behavior.—Occasionally solitary individuals are encountered along trails or in marginal situations but, as a rule, where there is one squirrel, others are not far away. Mountain meadows echo with the calls of alarm or warning passed on from one squirrel to others when a stranger intrudes. Many of these populations consist of family groups; instruction and discipline by the adults, playing among the young are as commonplace as in many species. The Columbian ground squirrel does seem to be more sociably inclined than most other American squirrels.

In 1955, chance provided an opportunity to observe a family of ground squirrels outside our kitchen door at the Many Glacier Ranger Station from June 22 to August 30. Within a 10-foot radius were seven burrow entrances, several partially concealed in clumps of willow (*Salix* sp.) and whortleberry (*Vaccinium membranaceum*). A plump adult female, patently lactating, frequented this site and cruised over a surrounding area of about 70 feet in radius; she was first observed on June 23, and regularly thereafter until August 14. On June 24 two others were also present—one taken to be an adult male, the other a yearling. Three juveniles appeared on June 28, all emerging from an eighth burrow about 10 feet distant from and somewhat smaller than the rest. On subsequent days other juveniles put in an appearance and the family group ultimately comprised the two adults and seven young, all frequently seen in the area at one time. One juvenile was noticeably smaller than the others; another, of a particularly independent disposition, often stayed at a distance from his mates and foraged separately. On many occasions, however, all seven young played and fed together amicably. At times there was some evidence of a "peck order" among the juveniles, but usually food was abundant and there was little indication of intolerance or dominance among the young squirrels.

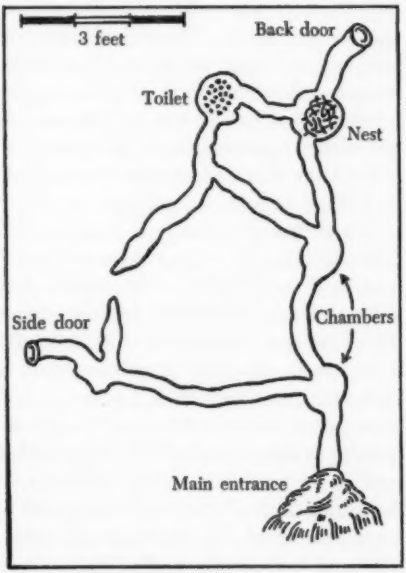

FIG. 3.—Plan of a winter den near Piegan Pass (7,000 feet) excavated on 27 July 1917. (*After Bailey, 1918.*)

Tragedy suddenly struck this group late on the afternoon of July 3. All the young were abroad, foraging and exploring, when the mother appeared, much

agitated. She darted hurriedly back and forth around the burrow most used by the young, called continuously in alarm, and dispersed her young in all directions. Presently a large weasel (*Mustela frenata*) emerged from another burrow, looked about and rapidly retreated; about 15 seconds later it appeared from another burrow and darted off to a nearby stand of young lodgepole pines. Within a half a minute the two adult squirrels reappeared, much alarmed; they frantically investigated the several burrows, calling constantly on a high-pitched note as they circled the area. Surprisingly, in a minute or so the weasel returned, carrying by its back a dead young squirrel, and disappeared with it down the burrow customarily used by the young. The weasel was not seen again, but the two adult squirrels promptly set up a search for the young, calling loudly. From all directions the young gradually appeared. The mother disciplined them, manually and vocally, and herded them into a group—all but the independent individualist! She kept them strictly away from all burrows, maintaining a constant low chatter and staying close by while the father furiously beat about the cabin and the adjoining woods. One juvenile returned from across a road, at least 50 yards from the home colony. After about 20 minutes six young were accounted for. By 7:15 PM they all disappeared, to spend the night in some unknown spot. The next day there remained four young squirrels and the two adults. The weasel was reported leaving the colony in the morning, and was not seen to return; that night all the squirrels retreated into their burrows about 6:00 PM. The six squirrels remained thereafter, although the adult male often was not seen for several days at a time. Once more, on July 6, the weasel appeared from one of the burrows and later left the area. How long it had been there, or whether it returned, is not known. Apparently it had made no further kills in this colony.

When first observed, all nine squirrels in this group were extremely wary. The adult female, at first, retreated to a burrow at the slightest disturbance and remained there for 15 to 20 seconds before timidly venturing forth again. She collected bread offered to her but carried it below ground before consuming it. This extreme caution lasted only briefly; bread was eaten on the spot within a day or so. By July 10 she accepted food from the hand, as did the young, and even permitted herself to be patted while eating. In another ten days all the squirrels were quite tame, though the adult male never abandoned caution as fully as the others. All ate from the hand, some came at a whistle, and several readily entered our cabin for food. On August 20 this behavior altered radically. The adults had disappeared by this time but the young were unduly wary and acted like wild animals again. They did gingerly accept food from the hand but went into their burrows before eating it. This changed attitude may have related to their approaching maturity or, more likely, to their imminent period of dormancy, their greed being largely satisfied and their bodies well fattened. As late as August 22 one stunted individual from a different group, still only about two-thirds grown, was readily accepting food from the hand and lapping milk from a saucer.

The initial seven burrows in the immediate vicinity increased to 14 during the summer, through the efforts of both adults and juveniles. Only four of these had adjoining mounds of excavated earth, and of the four, half contained only a few cupfuls of soil. The two burrows used principally by the young were somewhat smaller, at the entrance, than the others. In addition, two large burrows were constructed at the edge of the pines 60 feet to the east. They were probably intended as winter quarters for some of the old residents. As early as July 3 the adult female was seen carrying stalks of dry grass into one burrow; this activity continued for over a week and involved three different burrow entrances, including the one frequented by the juveniles and one of the new burrows at a distance near the pines. Soon after this the adults disappeared, presumably to their winter quarters for a prolonged stay. The young continued active about the area until August 30.

Breeding.—The most thorough study of breeding in the Columbian ground squirrel is that by Shaw (1925*a*) at Pullman, Washington, and my observations add very little to it. Mating occurs soon after the adults emerge from hibernation in April or May. The gestation period is about 24 days. The young are born early in May at the lower levels and perhaps as much as a month later at high elevations. Howell (1938) reported the unusually late record of a female carrying three embryos on June 24, 1895; this was at Nyack (3,300 feet) on the southern boundary of the Park. There are from 2 to 7 young, averaging about 4, per litter. Only one litter is raised each year. The newborn young are naked, quite helpless, with eyes and auditory meatus closed, and approximately 9 grams each in weight. But development is rapid and in about four weeks they are able to leave the nest.

Growth and development.—In the colony at Many Glacier, in 1955, the young were first noted above ground on June 27 (though they may have ventured abroad somewhat earlier). On this date they were far less than half grown but were well furred and able to get about under their own power. They probably were not yet completely weaned. All emerged from one burrow and none moved further than 5 or 6 feet from it. They showed very little independence, but stayed closely pressed to the ground, creeping along in an awkward fashion rather than running or jumping, and they made no attempts to perch erect. They did some exploratory nibbling on the foliage of grass and nearby shrubs. By July 3 they were eating a variety of wild foods and cruising much further from their burrow. On July 6 they were learning to sit up on their haunches and were first heard making rather crude attempts to call; also on this date they were first noted trying to burrow and they made occasional unsuccessful efforts to climb up stumps and low bushes. Four days later they were noticeably larger and far more confident in their actions; some ranged regularly across the road 50 yards away. They now called more frequently, sampled a wide variety of herbs and shrubs, and were able to burrow and sit up with ease. Much time was spent playing among themselves. Soon after this the young took food from the hand; at first they retreated to consume it,

but in a few days they stayed to eat it on the spot. By the end of July the young were nearly full grown. They again became wary in their actions; they still accepted food, but returned to their burrow to eat it.

At the higher levels development is retarded in consequence of the later dates of emergence and breeding. At Grinnell Glacier, for example, the juveniles were only about two-thirds grown on August 22. But in the following week they grew at an astonishing rate and appeared nearly full grown by the end of the month, with considerable accumulated fat to tide them over the coming winter. The combination of a late spring and an early winter, however, might well be disastrous for these squirrels.

In this connection, observations elsewhere in Montana were made by Moore (1937). He was concerned with breeding rates at different locations and found that the date of first appearance of the young above ground was delayed one day by an increase of 100 feet in altitude, and two weeks by an increase of one degree in latitude. Ground squirrels born at the highest elevations had insufficient time to mature fully during their first season. Moore concluded that the optimum elevation for development—as indicated by the largest squirrels, the fewest barren females and the largest litters—was at about 4,500 feet.

Although able to shift for themselves at a few months of age, full growth is not achieved until the second season. Breeding does not normally take place until a year, or frequently two years, of age. The oldest known specimen, an individual raised from birth in an outdoor enclosure, reached four years of age (Shaw, 1925*a*); it may have lived longer, but this was not stated. This was near Pullman, in eastern Washington.

Populations.—Although this species is widespread and conspicuous throughout most of the Park, it seems to reach its greatest numbers in the alpine meadows. No attempt was made to measure a population precisely, but an idea of the numbers involved may be gained from a few fortuitous observations in 1955. The weather was clear on each occasion. On August 2, along the Going-to-the-Sun Highway which runs 49 miles from the St. Mary River to West Glacier, crossing the Continental Divide at Logan Pass (6,654 feet), I counted 14 ground squirrels recently killed by traffic. On August 4, over a 17-mile stretch of the same highway from Logan Pass to the St. Mary River, I counted four fresh roadside kills; this, however, was at 6:00 AM—and the road had been closed at Logan Pass since 8:30 the previous evening because of fog early in the night. Certainly traffic had been light since then.

More reliable estimates of numbers may be obtained from living animals. Ground squirrels occur along the length of the 4.5-mile trail from the Swiftcurrent Campground to Iceberg Lake; the upper 1.8 miles, above Ptarmigan Falls, are largely in the Hudsonian and Alpine zones. On July 14, I flushed 21 ground squirrels from this trail, 16 of them above Ptarmigan Falls. On August 11, noting the squirrels that flushed along this trail within 10 feet on either side, I counted 19 in the entire distance, 12 of them above the falls. On this rather

precarious basis, and by dint of some dubious mathematics, I reach the approximate figure of 1.7 squirrels per acre on this 4.5-mile course.

The relatively simple burrow systems at higher elevations, particularly at or slightly above timberline where soil is sparse, are not capable of supporting as many squirrels as systems lower down. This circumstance possibly has a bearing on the social life of the animals, those at higher levels being inclined to a more solitary existence. In turn, this may be reflected in a lower breeding rate at high elevations—an advantage to the species in view of the smaller quantity of available food. In short, the social habits and the populations of these colonial animals vary in relation to the carrying capacity of their environment.

Foods.—A great variety of food is consumed, chiefly of a vegetable nature. The stomach usually contains a mass of finely comminuted green pulp with bits of root fibers, bulbs, stems, flowers, seed capsules or insect remains. Early in the summer green, leafy vegetation comprises the bulk of the diet and includes nearly anything available—wild and cultivated grasses, sedges, the foliage of strawberry, whortleberry, willow, buttercup, dandelion, corn lily, bear grass, balsamroot, lupine, pentstemon, ragwort and wild rose. Such bulbs as those of camas, wild onion and glacier lily are also relished. Later in the season fruits and seeds are consumed in large quantities, including currants, gooseberries, strawberries, thimbleberries, serviceberries and whortleberries. In cultivated areas the stems and heads of such plants as clover, oats, rye and barley are eaten, as well as the vines of potatoes and legumes and such crops as lettuce and carrots.

A small amount of animal matter may also be eaten. Grasshoppers, cicadas, beetles and caterpillars are sometimes taken, and fish may be eaten if the habitat borders a lake (Howell, 1938). On one occasion I observed a ground squirrel carrying a dead *Peromyscus* into its burrow—presumably a mouse I had trapped in the cabin the previous night, and discarded in the nearby woods. Handouts at picnic areas are never disdained; bread, potatoes, meats, cheese and oranges are eaten readily. The squirrels will sometimes fight for bits of chocolate or candy.

During their active period, the squirrels consume large amounts of food daily. In one case (Shaw, 1925*b*) the food eaten in one day amounted to 17.2 per cent of the body weight. As the season advances the squirrels feed voraciously in preparation for the coming period of dormancy. Great layers of fat accumulate beneath the skin and around the viscera. Some squirrels, during the last few weeks before hibernating, appear to nearly double their weight and become so fat they can scarcely waddle, their bellies literally drooping to the ground as they stand erect. They rely almost entirely on this stored fat during their long hibernation, for the storage of foods in their burrows is not the custom.

Females and juveniles almost never have a food reserve in their winter quarters, but old males may. Shaw (1925*c*) pointed out that these caches, of

moderate size, consist of *wild* seeds or bulbs, even when in an area of cultivated crops. Usually only one kind of food is stored in one cache, and this is not touched during the winter but saved for the time of awakening in the spring, when little else may be available—for the old males may emerge from their winter quarters weeks before the others.

Dormancy.—One of the most remarkable traits of the Columbian ground squirrel is its long and erratic period of dormancy, in which it rivals the dormouse or *Schläfer* (Gliridae) of the Old World. This inactive period, variously referred to as hibernation and estivation, probably partakes somewhat of the nature of each. Long before winter seems imminent the squirrels disappear into their hibernation dens, which may be part of a larger system of burrows or may be separate and remote. At any one locality the old males disappear first, then the old females, and finally the young of the year, perhaps several weeks later. The sleeping chamber itself is effectively sealed off by a plug of earth some 2 feet long. Here the squirrel curls up tightly, lying vertically on its back with head tucked into its belly and partly covered by the tail, and sleeps without eating and, apparently, without awakening for many months. It is in a torpid condition; its temperature drops from the normal 98° to about 40°F. (Shaw, 1925*d*). At the proper time in spring it emerges by digging straight up, placing the soil removed behind it in the burrow, so no loose earth appears at the entrance. Often, at the higher elevations, it is also necessary to tunnel up through packed snow several feet deep. The males emerge in spring a week or two before the females.

Oddly enough, the squirrels at lower altitude disappear in the autumn considerably earlier than those high up. In 1955, the last adult was seen at the Many Glacier area on August 14; at Grinnell Glacier a dozen were still active on August 31, but only three were seen along the trail to the glacier, all above 5,600 feet. Late summer in 1955 was unusually dry. In 1954, however, when rainfall was more nearly normal, squirrels were active at the Many Glacier area until August 30 (and one lone individual was noted at the hotel on September 6); they were seen at Iceberg Lake on September 2 and at Grinnell Glacier on September 3, and possibly were active even later at these sites which were not visited subsequently. Occasionally a few near timberline may still be abroad in early October. Miller (1938) has pictured the general situation as follows:

> In the vicinity of Lake McDonald, at an elevation of 3,200 feet, the Columbian ground squirrels went into hibernation about August 21. The Apgar lookout reported seeing the last ground squirrels on August 27; the last two on Logan Pass were seen on August 30. Young squirrels were seen as late as September 10 at Grinnell Lake; this was a week later than they were seen at the Many Glacier camp.

Dates of spring emergence vary likewise. Those in the valleys usually appear by April or early May, depending on the weather, but the spring appearance may be delayed until June in the higher meadows. Again the males precede the females by a few days or weeks. On June 25, 1955, I first visited Iceberg

Lake; ground squirrels may already have been active there for some time. I found many burrows up through the snow, still several feet deep in many places; frequently the burrows were located in the depressions that form in the snow around the boles of firs. Squirrels were cruising everywhere over the snow, many of them several hundred yards from the the nearest bare ground, where they were foraging.

Observed periods of activity in Glacier National Park are indicated in Table 1. These are compiled from my own observations as well as from reports in the files of the Park Naturalist's office. The data—so far as they go—are reliable, but in using them a word of caution is in order. Times of appearance and disappearance vary considerably at any one locality from year to year, but dates of observations are seldom available for consecutive years. Furthermore, many remote locations are unmanned or inaccessible until after the ground squirrels' spring activity has begun; at others, the squirrels are still active at the time of an observer's last visit. Thus most dates in the table give, at best, an approximate indication of the total periods of activity of these squirrels.

It has been suggested by Shaw (1925*e*) that early spring activities are largely controlled by temperature alone, whereas hibernation is induced, not so much

TABLE 1.—*Observed periods of activity of the Columbian ground squirrel at different locations in Glacier National Park, Montana*

LOCATION	ELEV., FT.	LAST SEEN IN FALL*	FIRST SEEN IN SPRING*	AUTHORITY
Lake McDonald	3,167	15 Aug. 1955	14 Apr. 1947	Robinson
West Glacier	3,219	15 Aug. 1954	6 Apr. 1952 26 Apr. 1951	Berger Robinson
Logging Ranger Sta.	3,500	———	11 Apr. 1947	Lindahl
Polebridge	3,578	———	14 Apr. 1944	Beatty
Walton Ranger Sta.	3,860	———	22 Apr. 1945	Wedge
St. Mary Lake	4,473	———	14 Apr. 1949 13 May 1950	Barnum Beatty
Apgar Lookout	4,553	27 Aug. 1938	———	Miller
East Glacier	4,821	———	10 Apr. 1944	Barnum
Many Glacier	4,872	15 Aug. 1941 13 Sept. 1944	Late April or May	Robinson McIntyre
Grinnell Lake	5,050	24 Aug. 1940 10 Sept. 1938	24 June 1954†	Adams Miller
Two Medicine Lake	5,175	19 Aug. 1955	23 June 1954†	Manville
Iceberg Lake	5,900	2 Sept. 1954	25 June 1955†	Manville
Grinnell Glacier	6,200	3 Sept. 1954	18 July 1955†	Manville
Logan Pass	6,654	30 Aug. 1938	19 June 1955†	Miller
Sperry Chalet	6,730	19 Aug. 1954†	9 July 1954†	Luding
Swiftcurrent Pass	7,176	14 Aug. 1955†	9 July 1954†	Manville

*Where two entries appear, they represent the earliest and latest dates of record.
†Ground squirrels probably were active later (in fall) or earlier (in spring) than dates indicate.

by low temperatures or failing food supply, as by drying of the vegetation. This is more pronounced in the valleys, where the longer time available for accumulating fat is probably another factor in the earlier disappearance of the squirrels. In the vicinity of Pullman, at an elevation of 2,500 feet, the squirrels spend seven to eight months per year in a dormant condition. They leave their hibernation dens in February or March; estivation begins by July 29 in dry seasons and by August 11 in wet seasons. Within 12 miles to the west, in the Canyon of the Snake River at an elevation of only about 600 feet, this schedule is advanced by nearly a month (Shaw, 1925*d*).

In the Bitterroot Valley, Ravalli County, Montana, Howell (1938) stated that the species was last seen on August 25, 1909, and first seen on March 6, 1910—a dormant period of 193 days. Howell felt that "the date of beginning estivation is determined chiefly by the ripening of the vegetation and consequent reduction of the moisture content in their food, and in part also by the accumulation of fat in the body."

In Idaho, Davis (1939) stated that the period of quiescence averaged 204 days for males and 220 days for females. He calculated, on the basis of number of daylight hours in summer in Idaho, that a squirrel may have available "no more than 23 per cent of the year in which to eat enough food to maintain life during the remaining 77 per cent of the year." The longest known period of dormancy, cited by Shaw (1925*e*), was 238 days for a young female.

In Kootenai County, Idaho, Rust (1946) believed that "the time of the spring emergence depends on the exposure, weather conditions, and the amount of frost in the ground." The feeding period at lower levels averaged 130 days, from March 20 to August 1; extreme dates of activity were January 16, 1933, and August 15, 1944.

These variations with respect to climate and elevation, as well as individual variations within the same local population, are somewhat parallel to those reported for the California ground squirrel, *Citellus beecheyi*, by Fitch (1948). At an elevation of 1,100 feet, in the San Joaquin Valley, many adult females were inactive from early summer until December or January; within 20 miles, but at 4,500 feet elevation, this species hibernated from November 1 to April 1.

Local distribution.—These squirrels occur widely in suitable habitat throughout the Park on both sides of the Continental Divide. Altitudinally, they range regularly from the elevations of the Flathead River (3,050 feet) to such high passes as Piegan (7,230 feet), Logan, Gunsight, Marias and Swiftcurrent, as well as on Flattop Mountain (7,500 feet) and Boundary Peak and at the Sperry Chalets and Grinnell and Blackfoot Glacier (6,879 feet). Although avoiding the heavily timbered areas, they still do not venture far above timberline. Exceptional are those cases where they occur, sometimes regularly and in fair numbers, at such manned summits as Brown Mountain (7,041 feet) and Swiftcurrent Mountain (8,300 feet). Edward Moore, the lookout on Swiftcurrent Mountain in 1952 and 1953, reported that at least twenty came from some distance (even up the cliff) for food at the summit (Plate II).

Bailey (1918) found these squirrels widely distributed except that "none were seen in the Kennedy or Belly River valleys." They still are absent (or extremely scarce) in the latter valley, which heads up in the lee of the Continental Divide and runs generally northeastward some 15 miles before it leaves the mountains for the Canadian prairies. Mantled ground squirrels (*Citellus lateralis*), chipmunks (*Eutamias* spp.) and pocket gophers (*Thomomys talpoides*) are well established in this valley; perhaps competition by them has prevented settlement by the Columbian ground squirrel. At lower levels there also occur, rarely, the thirteen-lined ground squirrel (*C. tridecemlineatus*) and the Richardson ground squirrel (*C. richardsoni*); there is evidence that the latter is being gradually replaced, from other directions, by the Columbian ground squirrel.

On August 9, 1955, I traveled the length of the Belly River Valley, from its southern rim at the Ptarmigan Wall (7,500 feet). This wall is pierced, some 100 feet below its crest, by a 50-foot-long tunnel designed to expedite travel by pack horses. On the southern face of the wall, Columbian ground squirrels were seen and heard on the scree slope up to within 200 vertical feet of the tunnel. On the northern side none were seen, but I heard familiar chirps and whistles in several locations and saw typical holes and diggings in grassy areas beside the trail within half a mile of the tunnel. On August 24, Walter Chance reported seeing what he took to be a Columbian ground squirrel somewhat further below the tunnel, and close to timberline, in the Belly River Valley. Mountain goats are known to use the tunnel; probably marmots, porcupines and others also do. Possibly the Columbian ground squirrel, by this means, is slowly colonizing this valley from the south.

Enemies.—These squirrels are tempting morsels for many kinds of predators. In the lower areas, badgers frequently dig them out of their burrows; in the high country, grizzly bears tear up large tracts of sod in attempts to get at them. In the latter case, perhaps the bears are most successful during September and October when the squirrels are already in a torpid state and the bears themselves are aiming to fatten up before they go into hibernation some two months later than the squirrels. On two occasions I found ground squirrels lying dead along a trail with no apparent injury as the cause of death; another time I found one that was badly mangled, the predator apparently interrupted at his meal by my arrival. Weasels, of several species, undoubtedly account for many squirrels. Other animals known to prey on them include coyotes, foxes, bobcats, cougars, golden eagles and hawks. It is small wonder that these creatures, ever alert and wary during their waking hours, give the impression of animals accustomed to being constantly hunted.

Economic importance.—In this section of the Rocky Mountains the Columbian ground squirrels are of no great economic significance, though they play an important role in the food chains of many predators. In the agricultural districts immediately to the east they have been considered pests because of their damage to grains, clover and pasture lands; in some spots they have

been all but exterminated by extensive poisoning and shooting. Within the Park they are protected and so become abundant and very tame in many places, sometimes to the point of constituting a nuisance about camps or causing injury to the meadows. About campgrounds, hotels and picnic areas they serve the useful function of scavengers, but also they are prone to raiding food supplies left unattended. Those who have tested their edible qualities pronounce them the equal of any tree squirrel, a young specimen resembling rabbit or chicken. Their work as cultivators of the soil has not been stressed but certainly their burrowing activities, especially where many are congregated, must be of considerable value in irrigating and aerating the soil; in some cases, these burrows in proximity to irrigation ditches have caused washouts. In the Park these squirrels seem to pose no special health hazard, but in the Bitterroot Valley they are regarded as an important host of the spotted fever tick (Birdseye, 1912) and in Oregon they have been implicated in plague infection (Meyer, 1936). Finally, mention should be made of a very positive function but one difficult to appraise—their aesthetic value by virtue of the pleasure they afford to many thousands of tourists and others.

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My data were gathered in Glacier National Park while serving as a ranger-naturalist at the Many Glacier area. I am grateful to M. E. Beatty and D. H. Robinson for providing the time necessary for field investigations, and for access to the files in the Park Naturalist's office; to Walter R. Chance for assistance in the identification of plants and for other favors; and to many other friends and colleagues who kindly contributed information not otherwise available.

SUMMARY

The natural history and status of the Columbian ground squirrel, *Citellus columbianus*, in the region of Glacier National Park, northwestern Montana, are reviewed from observations during 1954 and 1955. This species is abundant and widespread throughout most of the Park. It attracts the attention of the casual visitor by its general activity and is of special significance to the biologist because of many interesting habits. Particular details are presented pertaining to its habits, home site, social behavior, development, populations, dormancy and local distribution.

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THE REPRODUCTIVE CYCLE OF THE MALE ARCTIC GROUND SQUIRREL

BY ORMOND G. MITCHELL[1]

The sexual rhythmicity of mammals has long been a subject for investigation. Many of the hibernating rodents which have a sexual rhythm exhibit annual aspermia. Among these the thirteen-lined ground squirrel, *Citellus tridecemlineatus* of the midwestern United States, has been studied extensively. Johnson *et al.* (1933) and Wells (1935), among others, have demonstrated the histological changes accompanying the normal reproductive cycle as well as interesting experimental modifications. The arctic ground squirrel, *Citellus undulatus*—the northernmost representative of the genus in North America—is also known to breed only once a year, shortly after emergence in the spring (Mayer, 1953). Emerging in May, the animals must breed, rear their young and prepare for the long ensuing hibernation period by late September or early October.

Since little is known concerning the reproductive cycle of this squirrel, the following study was undertaken in an effort to correlate the histological changes observed in the testes with the relatively short activity cycle.

I wish to thank Dr. William V. Mayer of the University of Southern California for the opportunities afforded me as his assistant during the course of the life

[1] Recipient of an honorarium in 1957 for this paper.

history studies conducted on the arctic ground squirrel. These studies were supported in part by the U.S. Air Force under Contract No. AF 18(600)-843 monitored by the Arctic Aeromedical Laboratory, Alaskan Air Command, Ladd Air Force Base, Alaska.

Materials and methods.—The ground squirrels utilized in this study were collected from two regions of Alaska. One series, collected from June 18 to July 31, 1953, consisted of seven adult animals from the Umiat and Meade River study areas on the Arctic Slope. The second series of adults, consisting of six animals, was collected from May 13 to June 27, 1956, from the Paxson Lake study area at Mile 3.45 on the Paxson-Cantwell Road south of the Alaskan Range. The juvenile series was collected at the Meade River site from the time of the first emergence from the natal burrow noted on July 11 until August 1, 1953. Four animals were chosen for study from 22 juveniles collected during this period. These were selected at approximately one-week intervals on the basis of size increase. The approximate ages of juveniles were estimated by comparing the field measurements and weights with those of known-age laboratory-raised litters.

The testes were removed intact, cut, fixed in Bouin's fluid and later transferred to 70 per cent ethyl alcohol for storage. The gross testicular measurements were made on this preserved material. After being embedded in paraffin, the testes were sectioned at 10μ and stained with Weigert's hematoxylin and fast green. Tubule measurements were estimated by averaging ten of the most rounded tubules near the periphery of the testis. The gross measurements of the adult testes as reported are averages of both testes. The photomicrographs were made with the kind assistance of Mr. Lloyd Matlovsky.

Observations.—Paxson Lake Adult Series: The first animal observed in the spring of 1956, on May 13, had scrotal testes measuring 10 mm. in total length, 6 mm. in width and 5 mm. in breadth. The seminiferous tubules were rounded, in contact with one another and averaged 104.8μ in diameter. The basal membrane was lined with spermatogonia and toward the center of the tubules were many primary spermatocytes with nuclei in varying stages of development. In many of the more enlarged tubules, which contained a few secondary spermatocytes, lumina were forming (Plate I, *A*).

On May 20 the testes measured 16 mm. in total length and the epididymal tubules were filled with sperm. The seminiferous tubules were 153.7μ in diameter and exhibited active spermatogenesis. They contained many sperm clumps, spermatids and nurse cells (Plate I, *B*).

One week later, on May 28, sperm were still present in the epididymis even though many of the seminiferous tubules had a spent appearance. The tubules measured 148.8μ in diameter and many contained cellular debris and spermatids which filled the lumina. Spaces were present between the tubules which were angular in appearance and had a wrinkled basilar membrane.

No sperm were noted in the epididymis on June 4. Many of the seminiferous tubules contained cellular debris or were filling with a vacuolated fibrillar

matrix. The most prominent cell was the spermatogonium and only rarely did a tubule contain residual sperm clumps or spermatocytes (Plate I, *C*).

The tubules of testes collected on June 15 contained only spermatogonia and Sertoli cells oriented on the basal membrane. The lumina of the tubules were filled with matrix and the tubules appeared to have shrunken away from the basal membrane (Plate I, *D*).

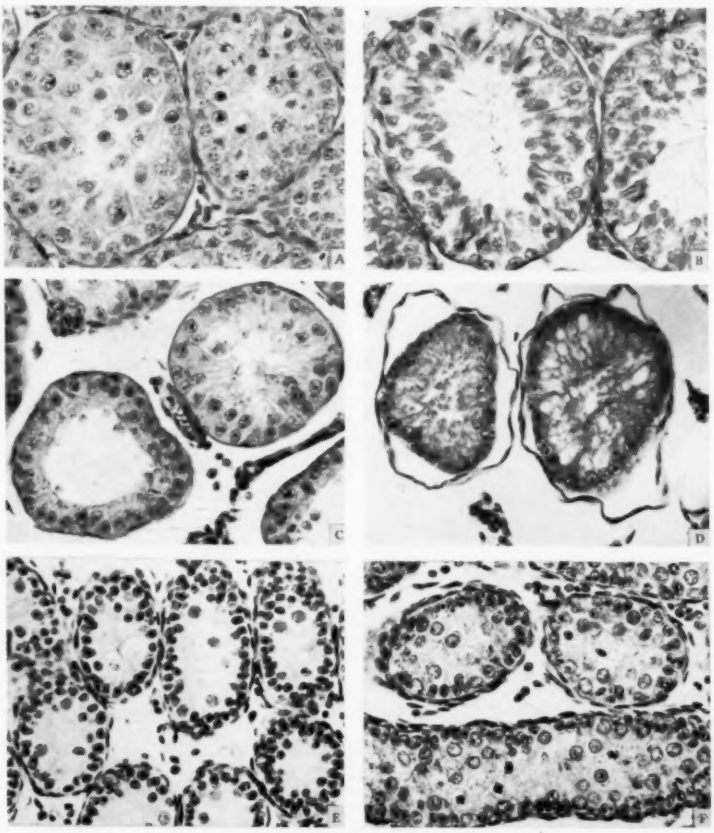

PLATE I

Sections of testes of adult ground squirrels. See Table 1 for dates and localities of collection. *A*, No. PL 1; tubules with primary and secondary spermatocytes, lumina forming within tubules. *B*, No. PL 2; sperm production in evidence, tubules with large lumina. *C*, No. PL 4; sperm production ended and matrix begins to fill tubules. *D*, No. PL 5; tubule shrunken away from basal membrane, base lined with single layer of spermatogonia and Sertoli cells. *E*, No. 275; early regeneration in inguinal testis, large primary spermatocytes in tubules. *F*, No. 286; inguinal testis, the nuclei of some primary spermatocytes containing chromatin masses resembling chromosomes. All × 250.

The final collection of this series was made on June 27, 1956. The testes were abdominal and measured 9 mm. in total length. The tubules measured 71.65μ in diameter and the lumina were filled with an acidophilic, vacuolated matrix. Mitotic activity was observed in the basal spermatogonial layer and primary spermatocytes were scattered through the tubules. The basilar membrane was closely applied to the rounded tubules.

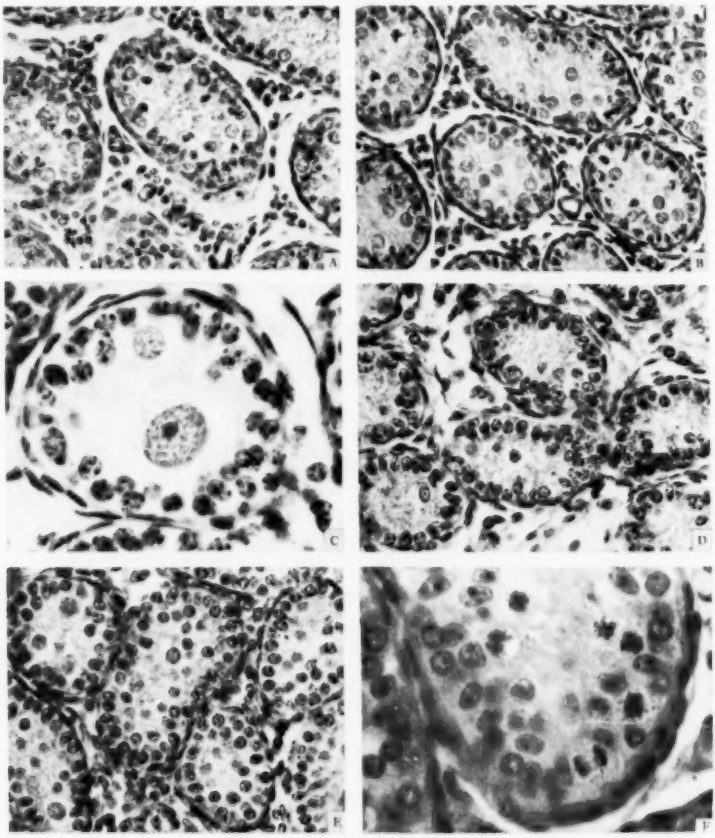

PLATE II

Sections of testes of adult (*A–C*) and juvenile (*D–F*) ground squirrels. See Table 1 for dates and localities of collection. *A*, No. 291; abdominal testes, tubules containing primary spermatocytes. *B*, No. 330; metaphase plate among basal spermatogonia in tubule at lower right. *C*, No. 275; nucleus of a large primary spermatocyte. *D*, No. 295; tubules containing a prominent basal layer of spermatogonia. *E*, No. 309; large nucleated cells within tubules in an animal of 27 days estimated age. *F*, No. 361; mitotic activity in the basal layer of spermatogonia. *C* and *F*, × 500; all others × 250.

MEADE RIVER—UMIAT, ADULT SERIES: The collection of the second series of adult testes began on June 18, 1953. The testes of the squirrel collected on this date were inguinal and measured 10 mm. in total length. The seminiferous tubules were filled with matrix and averaged 60.5μ in diameter. A single layer of spermatogonia was arranged evenly along the basal membrane. A few primary spermatocytes with granular nuclei were scattered inward from the spermatogonia and consisted of two types: one with a nucleus averaging 9.6μ, the other with large nuclei ranging from 12.8 to 16μ in diameter (Plate II, *C*). The larger nuclei contained prominent displaced nucleoli. The histological pattern of this testis resembled that observed in the juvenile testes at the end of July (Plate I, *E*).

On June 22 the testes were still inguinal in position and the tubules contained many primary spermatocytes with nuclei in spireme and pachytene stages of maturation. Rare large cells could still be seen (Plate I, *F*).

By June 29 the testes were abdominal and the tubules appeared to contain the same cellular elements as observed in the previous account (Plate II, *A*).

Through July the testes remained abdominal and, at the last collection on July 31, the tubules contained approximately the same cellular elements as were observed on June 29. The prominent cellular element was still the primary spermatocyte, the nucleus of which occurred in various stages up to the pachytene, although none were observed beyond this stage (Plate II, *B*).

JUVENILE TESTES: The first juvenile of the four selected for study was collected on July 11, 1953, as the mother moved the litter from the burrow to avoid a weasel; this was one week before another juvenile was collected from the study area. These observations, coupled with the estimated age of 25 days, indicated that the animal had not yet emerged from the natal burrow. The testes were abdominal and averaged 5 mm. in total length. The seminiferous tubules were solid and the lumina were filled with a homogenous matrix. The tubules averaged 68.9μ in diameter and were rounded and in contact with each other. The spaces between the tubules were filled with cellular material consisting of connective tissue and interstitial cells. Four cellular elements were observed in the tubules. Spermatogonia with typical ovoid or oblong nuclei averaging 6.4μ in diameter and containing one to three prominent nucleoli comprised the basal layer. Sertoli cells were also seen in this basal layer, but were not numerous. A few primary spermatocytes were located near the center of the tubules and contained ovoid nuclei which ranged from 9 to 10μ in diameter and, in rare instances, contained a small displaced nucleolus. The fourth cell type, which apparently consisted of large primary spermatocytes, contained nuclei which were as large as 14μ in diameter. These were ovoid, granular, and contained a single, large, displaced nucleolus (Plate II, *D*).

The only histological changes observed in the testes up to 42 days of age consisted of increased mitotic activity among the basal spermatogonia and an increase in primary spermatocytes. As many as 45 mitotic figures were observed

in the spermatogonial layer in one section. The last testis, collected on August 1, 1953, resembled the redeveloping adult testis of early June (Plate II, *F*).

Discussion.—The sexual cycle of the arctic ground squirrel may be divided into four parts: (1) a period of emergence from hibernation and maturation of the testes; (2) a period of sperm production and breeding; (3) a period of involution and cessation of breeding; and (4) a period during which the testes reascend into the abdomen and regeneration of the germinal elements begins.

Field observations have shown that the male squirrels appear as much as a week before the females. Similar observations have been made for the Piute ground squirrel (Alcorn, 1940), the golden-mantled ground squirrel (Mullally, 1953) and for the thirteen-lined ground squirrel by both Wells (1935) and Johnson *et al.* (1933). Johnson *et al.* reported that males emerged by the middle of March and the testes became scrotal in April. Mullally reported only five of nine newly emerged golden-mantled ground squirrels with scrotal testes. It appears that the week before emergence of the female is a period of maturation of the testes preparatory for mating. However, Wells (1935) stated that spermatids and sperm were present in the testes of the thirteen-lined ground squirrel prior to emergence from hibernation. In the arctic ground squirrel this does not appear to be the case. Corollary laboratory studies on hibernating squirrels in the colony maintained at the University of Southern California have shown that the testes do not become scrotal nor produce sperm until after awakening from hibernation. It does not seem reasonable to assume that all males are in the same reproductive condition on emergence since, because of cold weather, the animal may remain in its burrow active and warm for some time after awakening from hibernation.

The period of active sperm production appears to occupy a period of one week. This seems a very short time considering that the males are polygamous and, perhaps, should be extended to two weeks on the basis of observed sperm in the epididymis on May 28, even though production had ceased in many of the tubules. It is also possible that the animals begin breeding during the first week after emergence. A greater number of collections during this period are necessary to determine the limits of this stage. Mayer (1953) observed positive breeding in the field on May 24. This may give credence to the value of the observation of the sperm-filled epididymis on May 20. When one considers the known gestation period of 25 days and the estimated age of young animals on emergence during the second week in July, it seems evident that breeding must take place during the last two weeks in May.

The regression period begins during the first week in June, as evidenced by the condition of the testes collected on June 4. With the cessation of sperm production the tubules appeared to collapse, indicating some loss of mass. This may have been caused in part by the fixative. However, field and laboratory observations have shown that the testes become flaccid and soft, even though still scrotal, after a period of sperm production. The average tubule

TABLE 1.—*Summary of reproductive data utilized in this study; measurements for adults are averages of both testes, with epididymes removed*

NO. AND ESTIM. AGE (OF JUV.)	DATE COLLECTED	TESTES MEASUREMENTS, MM. (LENGTH—WIDTH—BREADTH)	AVE. TUBULE DIAMETER, μ
		Paxson Lake adults:	
PL 1	13 May 1956	10.0— 6.0—5.0	104.8
PL 2	20 May 1956	16.0—10.0—8.0	153.7
PL 4	4 June 1956	10.0— 6.0—5.0	95.7
PL 5	15 June 1956	12.0— 5.0—6.0	81.6
PL 6	27 June 1956	9.0— 4.5—3.0	71.65
		Meade River and Umiat adults:	
275	18 June 1953	10.0— 5.0—4.0	60.5
286	23 June 1953	9.5— 5.3—4.3	71.6
291	29 June 1953	10.0— 5.5—3.8	68.2
301	13 July 1953	10.5— 5.1—4.3	63.3
313	19 July 1953	9.3— 4.7—4.0	69.5
330	27 July 1953	9.0— 4.9—4.5	75.2
356	31 July 1953	8.0— 4.0—3.3	63.7
		Meade River juveniles:	
295	11 July 1953	5.0— 3.0—2.0	61.5
25 days		5.0— 3.5—2.0	
309	17 July 1953	5.5— 3.0—2.0	53.74
27 days		8.2— 3.0—3.0	
323	24 July 1953	6.2— 3.0—3.0	53.7
32 days		6.0— 3.5—3.0	
361	1 Aug. 1953	7.0— 4.0—3.5	67.6
42 days		8.0— 4.0—3.5	

diameter was also observed to decrease rapidly after May 28 (Table 1). Similar observations of shrinking and softening of the testes were reported for the fox squirrel by Allen (1942) and Brown and Yeager (1945) and were correlated with tubule degeneration by Kirkpatrick (1955).

The period of reascending of the testes and regeneration of cellular elements begins by the middle of June, as evidenced by the observation of inguinal testes on both June 18 and 22. The testes remain abdominal until the following spring. During the period of ascending the testes have been observed to become firmer to the touch, corresponding to the observed rounding of the tubules and the filling of the lumina with matrix. At this time there is an increase of spermatogonia, some of which begin to mature into primary spermatocytes. At least to the end of July, where our collections ended, the nuclei of these cells progress to what appears to be the pachytene stage of the first meiotic division. Similar observations of chromosomes in the nuclei of primary spermatocytes were made by Wells (1935) for the summer testes of the thirteen-lined ground squirrel, and for the pre-pubescent and post-rut testes of the fox squirrel by Kirkpatrick (1955). Wells further observed that these cells remained in this stage during

the summer and pointed out an increase in number, which he called a pre-hibernation primary spermatocytogenesis, prior to entering hibernation. Since the animal in hibernation is not metabolically active it is reasonable to assume that these cells are maintained throughout the winter in this stage and are the progenitors of a rapid sperm production in the spring. Mayer (personal communication) in recent work conducted in this laboratory has observed that cells of the pituitary which secrete the gonadotropic hormone are in a state of inactivity during periods of hibernation. This would further indicate a quiescence in the testes during hibernation.

Juvenile males emerge from the natal burrow with abdominal testes which apparently remain in this position until the following spring. The similarity of the juvenile testis to that of the redeveloping adult was also reported for the grey squirrel by Allanson (1933) and for the fox squirrel by Kirkpatrick (1955). This resemblance is easily explained when it is considered that, at the beginning of regeneration, the adult testis contains essentially the same primary germinative elements, spermatogonia, as does that of the juvenile.

The large primary spermatocytes (Plate II, *C*) observed in both the developing juvenile and regenerating adult testis are indeed curious. They have been reported in the juvenile testis of the thirteen-lined ground squirrel by Wells (1935) and in both juveniles and adults in post-rut in the fox squirrel by Kirkpatrick (1955). Both of these authors pointed out their resemblance to embryonic cells figured for the rat testis by Hargitt (1926) and to those in the testes of young bulls reported by Hooker (1944), who identified them as primordial germ cells. Kirkpatrick reported they contained no nucleoli and were of a "transitional nature becoming more like primary spermatocytes by a rearrangement of chromatin into denser masses and enlargement of nuclei." Dr. H. W. Mossman (personal communication) is of the opinion that they represent "abortive 'attempts' at spermatogenesis, 'attempts' which proceed farther and farther as the animal nears maturity. Until full activity and sperm production is achieved the products of each abortive wave of maturation are destined to undergo degeneration, just as are the crops of developing oöcytes in the ovary of a maturing female." The cells observed in the testis of the adult arctic ground squirrel possess prominent nucleoli, as seen in Plate II, *C*. The nuclear size of the normal primary spermatocyte in the later stages of development did not increase. These facts favor degeneration as the ultimate fate of these cells. However, until a critical cytological study is made, the character and density of the large spermatocytes remain in doubt.

SUMMARY

The sexual cycle of the arctic ground squirrel consisted of four periods: spermatogenesis prior to breeding, breeding, involution, and regeneration of the testes. Adult males emerged early in May with the testes in the early stages of spermatogenesis. Sperm production began one week after emergence and continued for approximately two weeks. Breeding took place during this period. Regression followed with tubular collapse and the testes became abdominal by the last week in June. Regeneration began immediately and progressed to the formation

of primary spermatocytes. The nuclei of these cells reached the pachytene stage of the first meiotic division. The arctic ground squirrel exhibited an annual aspermia beginning in June and extending at least to August 1. Young of the year had adominal testes on their appearance above ground during the second week of July. The seminiferous tubules of juveniles contained no lumina and resembled the early redeveloping adult testes. The histological changes within the testes were correlated with observed activities of the animal.

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Dept. of Biology, California State Polytechnic College, Pomona. Received March 27, 1957.

A NEW RICHARDSON'S MEADOW MOUSE FROM UTAH

BY DAVID I. RASMUSSEN AND NORMAN V. CHAMBERLAIN

In his "Mammals of Utah," Durrant (Univ. Kansas Publ. Mus. Nat. Hist., 6: 1–549, 1952) assigned all representatives of the species *Microtus richardsoni* (DeKay) from Utah to the subspecies *M. r. macropus* (Merriam). Subsequent collection of representatives of this species from Thousand Lake Mountain, the Fishlake Plateau, the Wasatch Plateau, the Wasatch Mountains and the Uinta Mountains of Utah and critical comparison of these specimens with paratypes of Merriam (N. A. Fauna, 5: 60, July 30, 1891) from Custer County, Idaho, show that specimens from Utah represent an unnamed subspecies.

All measurements are in millimeters and capitalized color terms are from Ridgway (Color Standards and Color Nomenclature, Washington, D.C., 1912).

Acknowledgments.—The authors wish to acknowledge with appreciation the loan of comparative material from Miss Viola Schantz, U.S. Fish and Wildlife Service. The illustrations for this paper were prepared by David I. Rasmussen.

Microtus richardsoni myllodontus subsp. nov.

Type.—Male, adult, skin and skull No. 13084, Museum of Zoology, Univ. of Utah; top of ridge, head of Boulger Canyon, 2 mi. NE Huntington Reservoir, 10,000 feet, Wasatch Plateau, Sanpete County, Utah; July 6, 1956; collected by David I. Rasmussen; original No. 143.

Range.—Thousand Lake Mountain, Fishlake and Wasatch plateaus of Central Utah, and Uinta and Wasatch mountains of Northern Utah. Northern limits unknown.

Diagnosis.—Size: Large (see measurements). *Color:* General appearance of upper parts dark Fuscous with moderate sprinkling of black hairs, other hairs bicolored, basal portion Blackish Plumbeous and tips Prout's Brown; sides lighter with tips Wood Brown; underparts with basal portion Deep Plumbeous, tips Pale Gull Grey; tail color variable, indistinctly bicolored with numerous white hairs on upper surface, small terminal tuft of white hair; fore and hind feet dusky becoming paler distally. *Skull:* Massive, angular; upper incisors long and procumbent; nasals short with anterior ends expanded laterally; anterior margin of maxillary plate of orbit straight; bullae large, flattened dorso-ventrally; occlusal view of mandibular molariform teeth shows nonconformity of linear arrangement of both medial and lateral borders of teeth succeeding the first molariform tooth (Fig. 1).

Measurements.—Measurements of the type and average and extreme measurements of four adult males, near topotypes, are, respectively, as follows: Total length, 231, 223.5 (215–230); length of tail, 74, 67.5 (65–74); length of hind foot, 25, 25.7 (25–28). *Skull:* Basilar length, 34.3, 33.76 (32.8–34.8); length of nasals, 9.3, 9.55 (9.2–9.8); zygomatic breadth, 20.5, 20.48 (20.0–20.7), least interorbital breadth, 4.6, 4.68 (4.5–4.9); mastoidal breadth, 15.5, 15.40 (15.1–15.9); basicranial depth over bullae, 11.3, 11.00 (10.8–11.2); alveolar length of upper molars, 8.2, 8.12 (8.0–8.3).

Comparison.—We have examined paratypes of *Microtus richardsoni macropus* and specimens from Utah and have found that specimens here assigned to *Microtus richardsoni myllodontus* differ from the aforementioned subspecies as follows: Upper incisors longer and more procumbent; nasals shorter with anterior ends more expanded laterally; external anterior margin of the maxillary plate of the orbit straight as opposed to concave; anterior opening of infraorbital foramen shorter and of different conformation (Fig. 1); tympanic bullae larger, more flattened dorso-ventrally; region of nasofrontal suture relatively smooth in profile contour as opposed to humped (raised) in adult specimens; occlusal

view of mandibular molariform teeth in irregular linear alignment, second molariform tooth slanted more medially, third molariform tooth slanted more antero-medially; lateral surface of condyloid process with thickened prominence.

In addition to the above cranial characters, specimens of *M. r. myllodontus* differ from paratypes of *M. r. macropus* in color as follows: Dorsal coloration with less ochraceous buff; underparts lighter gray; tail variable, whitish or indistinctly bicolored with grayish above whitish below as opposed to dark brown above; feet lighter, less brownish hair; general appearance of dorsal coloration grayish as opposed to brownish.

The differences in coloration may be a result of aging of the paratypes of *M. r. macropus* which were collected in 1890.

Remarks.—Representatives of the subspecies *Microtus richardsoni myllodontus* from various localities in Utah are completely recognizable on the basis of two cranial characters, namely the conformation of the anterior opening of the infraorbital foramen and the irregular linear alignment of the mandibular molariform teeth.

The species *Microtus richardsoni* reaches its southern limits of distribution on the Thousand Lake Mountain of south central Utah. The subspecies *M. r. myllodontus* is a montane form which extends its range southward by means of

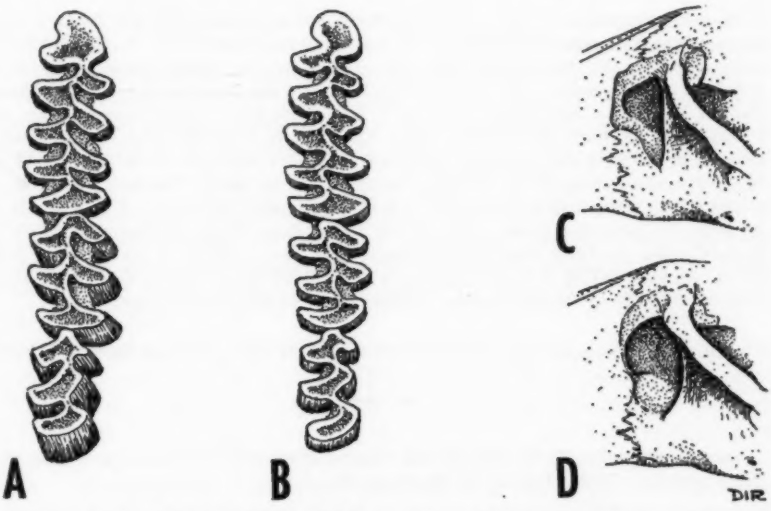

FIG. 1.—Occlusal view of right mandibular molariform teeth of (A) *Microtus richardsoni myllodontus*, UU 13078 and (B) *Microtus richardsoni macropus*, USNM 31451. Lateral view of left infraorbital foramen of (C) *Microtus richardsoni myllodontus*, UU 13078 and (D) *Microtus richardsoni macropus*, USNM 31451.

the high mountain plateau complex in Utah. *M. r. myllodontus* is physiographically isolated from *M. r. macropus* in Idaho by the valley of the upper Snake River. On the basis of physiography and ecological requirements a zone of intergradation between *M. r. macropus* and *M. r. myllodontus* probably occurs in the area of the Teton Range and Absaroka Range of northwestern Wyoming.

Examination of Richardson's meadow mice from the Wyoming-Idaho-Montana area when they become available should indicate the extent of intergradation which characterizes animals from the zone of gene exchange between the two subspecies. This zone of intergradation will probably be found to be primary in nature and the subspecific differences probably arose *in situ*. The clinal gradation of characters may be rather abrupt owing to the opposing population pressures, resulting from the large size of the populations, the wide geographical distribution of both subspecies, and the relatively narrow zone of contact between the two subspecies.

The subspecific name *myllodontus* is taken from the Greek words *myllos* meaning crooked or winding and *odontos* meaning tooth and refers to the alignment of the mandibular molariform teeth.

Habitat.—In Utah, the Richardson's meadow mouse is a semiaquatic mammal of montane streamsides. The type specimen was trapped in a well-defined runway in a spring-fed subalpine meadow among marsh marigold, *Caltha leptosepala* DC, and watercress, *Rorippa rasturtium-aquaticum* (L).

Specimens examined.—Total number 126, distributed as follows: IDAHO. *Custer County:* Salmon River Mountains, 9; Pahsimeroi Mountains, 6; Saw Tooth Lake, 6. UTAH. *Weber County:* Beaver Crk. South Fork Ogden River, 1; Squaw Flat, Monte Cristo, 10,000 ft., 1. *Salt Lake County:* Salamander Lake, Lamb's Canyon, 9,000 ft., 10; Wilson Fork, Millcreek Canyon, 1; Brighton, Silver Lake, 8,750 ft., 7; Alta, 9,500 ft., 1. *Uintah County:* 9 mi. NW Paradise Park, 11,000 ft., 1. *Sanpete County:* Mammoth R. S., 9,000 ft., 14; Head of Boulger Canyon, 10,000 ft., 4; Pleasant Crk. 7 mi. E Mt. Pleasant, 7,800 ft., 6; South Tent Pk., 11,100 ft., 2; Ephraim Canyon 15 mi. E Ephraim, 10,000 ft., 8; Seeley Crk. R. S., 9,800 ft., 9. *Emery County:* Huntington Canyon, 9 mi. NW Huntington, 8,000 ft., 11; Upper Joes R. S., 8,700 ft., 1; Lower Joes Valley, 7,800 ft., 1; Ferron Resv. 12 mi. W Ferron, 8,500 ft., 3. *Sevier County:* Lost Crk. Resv. 2 mi. E Boobe Hole Mtn., 9,300 ft., 2; Mt. Marvine, 9,200 ft., 11; Rockspring Crk. 1.5 mi. N Johnson's Resv., 9,000 ft., 6; Pelican Crk., 9,000 ft., 1; Fishlake, 8,750 ft., 2. *Wayne County:* Elkhorn G. S., 14 mi. N Torrey, 9,400 ft., 2.

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Answer from p. 12: At the 39th Annual Meeting of the Mammal Society at Washington, D. C., next June 22–24. For full details see p. 164.

THE EFFECT OF FLOODING ON A MARKED POPULATION OF *PEROMYSCUS*

By Howard McCarley

The effect of flooding on terrestrial populations of animals has been discussed in previous papers by Grinnell (1939), Blair (1939), Stickel (1948) and Rutherford (1953). Blair discussed the detrimental effect of stream-valley flooding on mammalian populations, while Grinnell discussed the effect of flooding on animal populations in general. Rutherford reported specifically on the effects of a flash flood on beaver populations. Stickel reported that flash flooding had no detrimental effect on a population of *Peromyscus leucopus*. Of these workers, only Blair and Stickel used traps before and after flooding to measure the animal populations and they reported somewhat different results.

Weather conditions in eastern Texas in the spring of 1957 were conducive to lowland flooding. While the amount of precipitation varied to some extent from one locality to another, the entire eastern Texas area received rainfall in excess of the normal amount. From January to April, 1957, this abnormal amount of precipitation was either absorbed by the soil or the runoff was effectively handled by the streams of the area. On the night of April 24, 1957, a 3.5–5-inch rain fell on the already saturated ground in Nacogdoches County, Texas. At about this same date both lesser and greater amounts of rainfall were falling elsewhere in the central part of eastern Texas. This general deluge resulted in a considerable amount of runoff which caused flooding on most of the smaller streams in the area. As this water reached the larger rivers, they too reached flood stage and in many places spread out onto the floodplains.

The present report deals with the effect of stream-valley flooding of both short and long duration on an identified and known population of *Peromyscus gossypinus* and *P. nuttalli*. This study arose out of a long-range study of the population dynamics of these two species which was supported by a research grant from the U.S. Atomic Energy Commission—Contract No. AT-(40-1)-1980. Roger Williams, Robert Timbrook and Henry Steitz served as research assistants on this project during the time the information contained in this paper was compiled. Appreciation is expressed to W. Frank Blair for reading and criticizing the manuscript.

For about 27 months prior to the above-mentioned flooding, these two species of mice had been studied in the field by live-trapping and marking the mice, releasing them at the site of capture and observing the dynamics and behavior of the two species. These mice were being studied on two study plots, each about 13 acres in size, three miles apart, and approximately 15–18 miles southwest of Nacogdoches, Texas. Each plot was surveyed in the form of a grid pattern with live traps located every 75 feet in parallel rows 75 feet apart with approximately 100 traps on each plot. Because of significant differences in type and extent of flooding on each plot it will be necessary to consider them separately; they have been designated as Plot A and Plot B.

Plot A is in a heavily wooded area on an upper terrace of the floodplain of the Angelina River about 18 miles southwest of Nacogdoches, Texas. This plot is about three miles from the river and is only rarely subject to any flooding from the river. The vegetation on the plot consists mostly of water oak (*Quercus nigra*), blue beech (*Carpinus caroliniana*) with a scattering of lesser numbers of other woody species. There are numerous topographic depressions and natural drainage pools on this plot. These drainage sites empty into Bernaldo Creek, a continuously flowing stream, which lies along one entire side of the plot. On the opposite side of the plot is a graded dirt road which forms a boundary between the mesic floodplain community and a more xeric upland type of community. The remaining two sides of the plot are continuous with the mesic floodplain forest.

This plot was almost completely inundated by a flash flood resulting from heavy rain on the night of April 24, 1957, on the watershed of Bernaldo Creek. Water spread over the banks of the creek and rushed over the study plot to a depth of 8 feet in some places. This rush of water completely disturbed the habitat, washing traps, logs and brushpiles away and depositing piles of drift in other places.

By April 26, the water had receded almost within the confines of the stream bed when a rise of the Angelina River backed water up Bernaldo Creek so that it again overflowed its banks, although this flooding involved little current. By May 3, this water had almost drained off the plot because of a drop in the floodstage of the river. This made it possible to enter the plot and reset and replace the traps. All traps were reset on May 3, 4, 5, 10, 11, 12, 24, 25 and 26.

Prior to the flooding on this plot, traps had been set earlier on the nights of April 7, 12, 13, 14, 20 and 21. Because of this trapping, it was known approximately what numbers of *P. gossypinus* and *P. nuttalli* were present on the plot before the flooding and where on the plot each mouse occurred. This population is shown by individuals in Table 1. A distinction is made between resident and transient individuals in this study, with a resident being defined as an individual caught two or more times but, if only twice, the times of capture must have been at least 20 days apart.

Table 1 shows that prior to the flooding 11 *gossypinus* were captured on the plot. Eight of these mice could be classed as resident individuals and three as transients. Of the eight resident individuals, five were recaptured after the flood during the period of 900 trap-nights mentioned above. Of the transient individuals present on the plot, none were ever recaptured. Of those *gossypinus* which were recaptured after the water had receded, all were caught in traps that were either inside or immediately adjacent to the home range that had been established by each mouse prior to the flooding. In this case home range was calculated using the method which Stickel (1954) calls the inclusive boundary strip method, as proposed and used by Blair (1940).

Table 1 also shows that 13 *nuttalli* were living on the plot prior to flooding. All of these individuals could be considered residents by the criteria mentioned

earlier. After the water receded, two of them were never recaptured and must be presumed to have been absent from the plot. Of the 11 individuals recaptured, seven were recaptured in traps which were within the boundary of the established home range. The other four were recaptured in traps that were either partly included in the established home range or in traps that were adjacent to the home ranges as established before the flooding.

It would thus seem that the population was affected very little on Plot A where flood water was present for an eight-day period. When the *gossypinus* are considered we find that 46 per cent of the total number present prior to flooding were still present after the water receded. When this is interpreted in terms of resident mice we find that the residents remaining after the flood were 60 per cent. All the *nuttalli* present were residents and 11 of 13 were still present after water was gone. This represents 84 per cent of the resident mice of this species. It would seem that in this case there was apparently

TABLE 1.—*Vital statistics of mice living on Plot A prior to flooding, number of captures prior to flooding, period of time in months and days lived on plot prior to flooding, depth of water over established home range and relation of captures after flooding to established home range (H. R.)*

NO.	AGE, SEX	NO. OF CAPTURES	PERIOD OF TIME ON PLOT, MONTHS AND DAYS	DEPTH OF WATER OVER HOME RANGE	RELATION TO HOME RANGE AFTER FLOODING
			P. gossypinus:		
189	ad ♂	28	2–21	6″–4′	Inside H. R.
207	ad ♀	5	2–21	2′–8′	Inside H. R.
210	ad ♂	2	2–11	3′–4′	Inside H. R.
212	ad ♂	7	2–4	1′–4′	Never recaptured
218	ad ♀	2	1–18	2′–3′	Never recaptured
222	ad ♀	7	0–29	3′–4′	Inside H. R.
225	ad ♂	4	0–17	2′–3′	Never recaptured
227	juv ♂	2	–2	7′–8′	Never recaptured
228	ad ♂	2	–3	3′–4′	Never recaptured
229	ad ♂	6	–7	2′–3′	Inside H. R.
230	ad ♂	1	–1	3′–4′	Never recaptured
			P. nuttalli:		
78	ad ♀	25	15–7	0″–3″	Inside H. R.
81	ad ♂	12	15–5	0″–1″	Inside H. R.
102	ad ♂	13	13–8	6″–2′	Adjacent to H. R.
103	ad ♂	2	13–8	1′–4′	Inside H. R.
148	ad ♂	12	5–11	6″–2′	Inside H. R.
154	ad ♀	4	4–21	1′–4′	Inside H. R.
157	ad ♀	25	4–14	6″–8′	Partly inside H. R.
159	ad ♀	12	4–11	6″–2′	Adjacent to est. H. R.
174	ad ♀	13	3–18	2′–6′	Inside H. R.
179	ad ♀	14	3–17	2″–4′	Never recaptured
185	ad ♀	6	3–16	2′–8′	Never recaptured
202	ad ♀	5	2–22	0 –1′	Inside H. R.
211	ad ♀	6	2–0	6″–1′	½ outside H. R.

very little mortality in either species that could be attributed to the effect of flooding. In addition to the previously marked mice of both species which were present on the plot after flooding, eight new *gossypinus* and one new *nuttalli* were captured. This represents a population increase of 4 per cent or one more mouse than was present prior to the flooding. This small increase is important because it means that the total population after flooding remained about the same as before flooding and certainly did not decrease.

It is also important that, of those mice (of both species) which were recaptured after the flooding, all were recaptured in areas that were either included in, or adjacent to, established home ranges. This suggests that these mice probably did not disperse from the plots during the flooding but instead lived in the trees that were present on the plot. This belief is supported by the fact that both species are at least partly arboreal. At other times traps have been set in flooded areas elsewhere in trees and on stumps and have produced about the expected number of *gossypinus* (McCarley, 1953). The effect of flooding of this duration on the mouse population is apparently not detrimental and is similar to the effect of flooding on other arboreal mouse species noted by Stickel (1948).

Plot B is of a somewhat different ecological nature from Plot A. It is located on a lower terrace of the floodplain of the Angelina River than is Plot A. It is also closer to the river and consequently more subject to the effect of river

TABLE 2.—*Vital statistics of mice living on Plot B prior to flooding and showing age, sex, number of captures prior to flooding, period of time in months and days lived on plot prior to flooding, depth of water over established home range and relation of captures after flooding to established home range (H. R.)*

NO.	AGE, SEX	NO. OF CAPTURES	PERIOD OF TIME ON PLOT, MONTHS AND DAYS	DEPTH OF WATER OVER HOME RANGE	RELATION TO HOME RANGE AFTER FLOODING
			P. gossypinus:		
125	ad ♀	4	2–20	1′–2′	Never recaptured
129	ad ♀	2	2–17	1′–2′	Never recaptured
133	ad ♂	7	2–11	1′–2′	Never recaptured
136	ad ♀	7	1–28	1′–2′	Never recaptured
141	ad ♀	5	1–02	1′–2′	Never recaptured
142	ad ♀	2	1–00	1′–2′	Never recaptured
144	ad ♂	3	–14	1′–2′	Never recaptured
145	juv ♂	4	–9	1′–2′	Changed H. R.
150	ad ♂	2	–2	1′–2′	Captured near sites of previous capture
151	ad ♀	2	–2	1′–2′	Captured near sites of previous capture
152	juv ♂	1	–1	1′–2′	Never recaptured
			P. nuttalli:		
105	ad ♀	10	4–7	1′–2′	Never recaptured
113	ad ♀	9	3–17	1′–2′	Inside H. R.

flooding than is Plot A. As on Plot A, there are numerous depressions and natural drainage areas but they are not as deep as on Plot A. One side of Plot B is limited by a small creek which is generally similar to Bernaldo Creek but which does not drain as extensive an area and is consequently smaller in size. The vegetation on Plot B is similar in species composition and dominants to Plot A, but generally the vegetation is more advanced from a successional standpoint so that there is more of an upper story of larger trees, mainly water oaks, with a correspondingly lesser amount of small woody and herbaceous vegetation on the floor of the forest. This plot is also close to an upland habitat type from which it is generally separated by a graded dirt road. Apparently, because of the slight difference in successional stage between Plot A and Plot B, the latter has consistently supported a smaller combined population of *gossypinus* and *nuttalli*. This is shown by Tables 1 and 2 for the month preceding flooding.

Plot B was inundated to a depth of about two feet on the night of April 24 by a flash flood similar to the one that covered Plot A, but a smaller amount of water was involved. Most of this water drained off by the afternoon of April 25 but, during the night of April 26, the flood on the Angelina River had reached such proportions that it swept out on the floodplain and completely inundated Plot B. This plot remained covered with water to a depth of two feet until May 16, 1957. This period of 21 days of flooding was considerably longer than the period of flooding on Plot A.

Prior to the flooding on Plot B, on April 24, traps had been set for the same dates given for Plot A. The population as known to exist on Plot B during this time is shown in Table 2. At this time 11 *gossypinus* were living on the plot, of which eight could be considered residents by the definition given earlier. Of these eight mice only one was recaptured when traps were set on the nights of May 17, 18, 19, 24, 25 and 26. The one resident mouse that was recaptured had completely changed his home range as established prior to flooding. This particular individual was a juvenile when first captured, before the flooding, and the change in home range in this case cannot necessarily be attributed to the effect of the water. Two of the three transient individuals were recaptured; both were taken in areas where they had been caught prior to the flooding.

Only two *nuttalli* were living on the plot prior to flooding. One was recaptured completely within the old established home range and the other was never recaptured.

It appears that the flooding on Plot B, where the water remained for a three-week period, was much more detrimental to the population than on Plot A where the water remained for only about a week. This is similar to the situation found by Blair (1939) on the floodplain of Bird Creek in northeastern Oklahoma. Before flooding on Plot B, 11 *gossypinus* were living on the plot either as residents or transients. After the water had receded, only three (27 per cent) of these mice were recovered. It could be argued that had the

traps been set for as many nights on Plot B (600 trap-nights) as on Plot A (900 trap-nights) more marked mice might have been caught. Additional trapping in June (800 trap-nights) substantiates the belief that all marked mice living on the plot were captured in May. The 27 per cent figure of recoveries of *gossypinus* on Plot B is much lower than the 46 per cent recovered after flooding on Plot A. On Plot B, in fact, only two out of ten resident *gossypinus* and *nuttalli* were recaptured after the flood. No new mice of either species were captured on Plot B during either May or June. Consequently, on Plot B there was a 70 per cent decrease in the total population of mice of both species after the flood waters had receded. Of course, some of this decrease can be attributed to normal mortality over a three-week period.

It would thus appear that the effect of flood water on populations of mice is not always as detrimental as reported by other workers, particularly Blair (1939). It seems that the effect of flood water on populations of *Peromyscus* is dependent, at least to a certain extent, on several factors. Arboreal and semiarboreal forms, such as *gossypinus* and *nuttalli*, tend to be least affected, as shown by this study and that of Stickel (1948). There also seems to be a tendency for individuals of these species to remain in their established home ranges. This is particularly true of flooding of short duration. Flooding of a duration of three weeks was detrimental to populations of *gossypinus* and *nuttalli*. Even in floods of this duration there seems to be a tendency for arboreal mice to remain in their established home ranges, rather than to disperse elsewhere.

SUMMARY

Extremely heavy rains in the spring of 1957 in eastern Texas produced flooding on nearly all streams in the region. This flooding covered two areas which contained marked mice of the species *P. gossypinus* and *P. nuttalli*. One area was inundated by a flash flood which was followed by a general flooding of eight days. The other area was inundated by a flash flood which was followed by a general flooding of a three-week duration. In these cases, the short-term flooding produced no detrimental effect on the mice present after the flood as compared with those before the flood. Flooding of a three-week period in a similar habitat produced a 70 per cent decrease in the combined population of the two species. There was a remarkable tendency on the part of the mice to remain within their established home ranges during the flooding on both plots. The supposition is that, since these mice are at least partly arboreal, they lived in trees while the areas were flooded.

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SEX RATIO, AGE CLASSES AND REPRODUCTION OF THE BLACK-TAILED JACK RABBIT

BY R. R. LECHLEITNER

The black-tailed jack rabbit, *Lepus c. californicus*, is locally abundant in the Sacramento Valley of California and is important as a game animal, a crop depredator and a carrier of diseases. It has adapted itself to the agricultural practices on both irrigated and nonirrigated lands. Despite its abundance and importance in this agricultural habitat, little information is available on its biology.

A population of this hare was studied from September, 1954, to March, 1956, on the Gray Lodge Waterfowl Management Area in Butte County, California. The area of about 6,800 acres is managed by the California Department of Fish and Game. Over 2,000 acres are ponds and marshes and much of the remainder is planted to crops such as rice, millet, barley and milo. Many miles of irrigation ditches and dirt roads contribute to the broken effect of the area. Some fields are left fallow and these, as well as the ditch banks and road sides, produce a cover of weeds. No detailed study of the soils on the area has been made but they are in general an adobe-alkali type. Most of the rain falls from October through March. Winter temperatures sometimes go slightly below freezing and summer temperatures often exceed 100°F.

The data in this paper are based on the examination of periodic samples of jack rabbits killed during each of the 18 months of the study. The method of collection was to walk through the fields during the afternoon, shooting at all hares raised within shotgun range. Of 435 hares examined, 355 were collected in this manner. Among the remainder, 26 were road kills, 25 were collected with a rifle, and 19 were from miscellaneous sources such as deaths due to disease and poison.

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of Vertebrate Zoology of the University of California at Berkeley provided me with the necessary equipment and funds. To these, and to others too numerous to mention, I extend my sincere thanks.

This paper is a contribution of the Department of Zoology and the Museum of Vertebrate Zoology, University of California, Berkeley.

SEX CRITERIA

The determination of the sex of a recently killed jack rabbit presents no difficulty, and it is not with such carcasses that the discussion here is concerned. It is sometimes helpful for the student of populations to be able to tell the sex of carcasses found in the field, even after all or most of the soft parts and the obvious signs of sex have been destroyed. Several authors have discussed sexual dimorphism in the pelvis of rodents and Dunmire (1955) emphasized its usefulness in population dynamics. There are sexual differences in the pelvis of the black-tailed jack rabbit, and within certain limits these differences may be quantified. In general, the pelvic girdle of the female is broader and flatter than is that of the male. Both innominate bones must be present and joined at the public symphysis to show these differences. Often the two bones are broken apart or one bone may be missing from old carcasses found in the field. Thus it is advisable to select differences which can be noted in one innominate bone.

The sexual dimorphism in the innominate bone of the jack rabbit appears to be the reverse of that found in certain members of the rodent genus *Microtus* (Dunmire, 1955) in that the pubic bone tends to be broader and relatively shorter in the female than in the male. Dunmire (1955) presented a method for expressing these relations graphically. This method is adopted here with certain modifications. Measurement *I* represents the shortest distance from the most posterior point on the ischium to the posterior edge of the acetabulum. Measurement *P* represents the shortest distance from the anterior ventral edge of the pubic symphysis to the posterior ventral edge of the acetabulum. The proportionate elongation of the pubic bone is then expressed as an index obtained by dividing *P* into *I*. Measurement *W* represents the narrowest width of the pubic bone along the symphysis. The method of taking these measurements is illustrated in Fig. 1, and the sexual dimorphism of jack rabbit innominate bones is illustrated graphically in Fig. 2 where *W* has been plotted against the index *I*/*P*. It can be seen that the separation of the sexes is not complete but is of a reliability suitable for most practical purposes. The data utilized in Fig. 2 included only those animals showing a complete fusion of the bony elements. When younger animals are included, the overlap between the sexes is great. Dunmire (1955) indicates that sexual dimorphism of the bones is conditioned by estrogen and testosterone. Since large quantities of these hormones are not available until the first period of sexual activity, the bones from younger animals may not yet have developed a distinguishable sexual difference. Although, as will be shown later, evidence indicates that certain of the jack rabbits in this population come into breeding condition before these bony elements fuse, the majority do not. It is advisable, therefore, when trying to distinguish the sex of animals by means of innominate bone conformation, to disregard all bones with open sutures, for their inclusion may lead to great error.

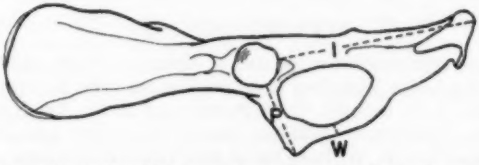

FIG. 1.—Side view of a jack rabbit innominate bone to show the measurements taken. See text for further explanation.

SEX RATIOS

The sex ratio of 389 jack rabbits in the kill sample was 198 males to 191 females, figures which do not differ significantly from the hypothetical 50:50 ratio. Further analysis by months shows that in no month does the sex ratio deviate significantly from equality, and there is no significant divergence from this ratio with any of the methods used to collect the hares, except perhaps with the rifle. The numbers here are small (14 males to 8 females) but suggest that this method may favor the collection of males. Especially during the height of the breeding season, males may be about more often during the day than females and are thus more available for collection with a rifle (Lechleitner, 1956).

On March 23, 1956, 46 jack rabbits were killed in a drive-shoot on Field 23 on the Gray Lodge Management Area. Preliminary counts indicated that approximately 63 hares were living in this field at the time. Of the 46 collected, 23 were males and 23 were females. Thus the sex ratio of the hares in this particular field at this period of the year was 50:50 as shown by this sample of about three-quarters of those known to be living there.

The prenatal sex ratio determined from 51 fetuses in 22 near-term females was 26 males to 25 females, a ratio not different from the postnatal ratio in the kill sample. It is therefore concluded that in the Gray Lodge jack rabbit population the sexes are equally represented.

Carcasses of jack rabbits were found throughout all months but occurred in greatest numbers during the fall and winter. Excluding hares killed by automobiles, 150 carcasses were found. The sex ratio of 114 of these was 60 males to 54 females, indicating that the mortality was equally divided between the sexes.

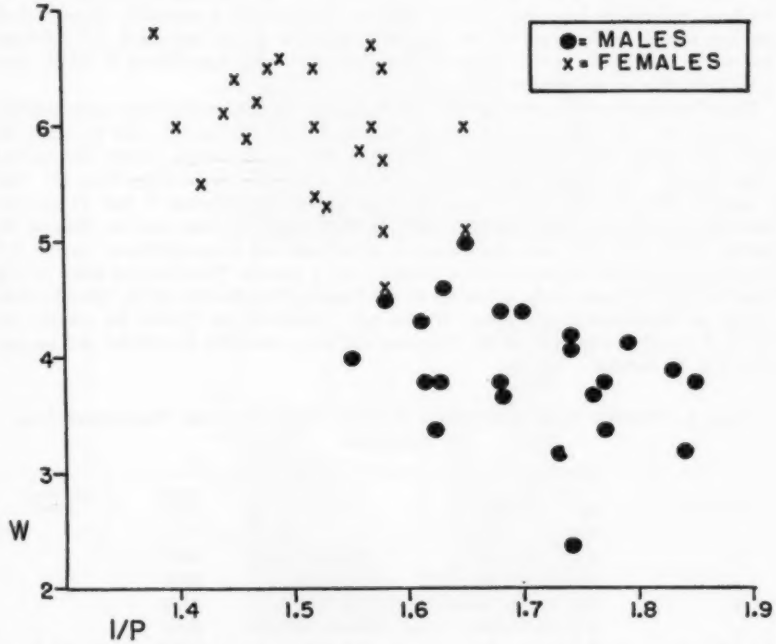

FIG. 2.—Separation of the sexes of jack rabbit carcasses by pelvis measurements. See text and Fig. 1 for further explanation.

AGE CRITERIA

Weight or size is only roughly indicative of the age of jack rabbits, and only until they are about seven or eight months old. Haskell and Reynolds (1947) have shown that jack rabbits reach adult weight at an average age of 32 weeks.

During the present study, three jack rabbits were captured as young and were raised in rather large enclosures. They were first fed canned cow's milk and then at about four weeks were weaned to commercial rabbit pellets supplemented with greens and carrots. The weight gains of these captive jack rabbits compare favorably with the average of weights of captive Arizona jack rabbits as determined by Haskell and Reynolds (1947) indicating that the two subspecies show similar growth.

Severaid (1942) showed that weight alone is not satisfactory for age determination of young snowshoe hares on a monthly basis after the first month. The evidence indicates that the same is true of the black-tailed jack rabbit. It is perhaps safe to assume that weight will indicate age with an accuracy of about two months up to approximately seven months when some of the animals reach a weight which lies within the range of variation of much older animals (Table 1).

The closure of the epiphyses of the bones may be used to indicate the age of a mammal for some time after its growth rate has slowed enough to be imperceptible, and a number of authors have used the closure of the epiphyses of the long bones to indicate age groups of various lagomorphs. In the present paper the hares are classified into age classes according to the degree of closure of the proximal epiphyses of their humeri as follows: Age Class 1, in which the epiphyseal area is represented by a definite groove because the cartilage has not been replaced by bone; Age Class 2, in which the epiphysis is essentially closed and all cartilage is replaced by bone, but the bone trabeculae are not yet organized and a definite line can be seen on the surface indicating the place of closure; Age Class 3, in which there is no indication of an epiphyseal line.

Two of the captive jack rabbits mentioned above were killed when they were approximately 11 months old, and the third when it was approximately 7 months old. The 11-month-old hares had humeri with the epiphyses closed but with a faint though definite line present (Age Class 2). The 7-month-old hare had a decided epiphyseal groove (Age Class 1). Thus it appears that the epiphyseal groove disappears sometime between 7 and 11 months. Since the size of the groove was quite large in the 7-month-old hare and the lines on the humeri of the other two were quite faint, it is probably not unreasonable to assume that the time of the closure of this groove is betwen 7 and 9 months. This does not differ greatly from the time of closure of the epiphyses on this bone in the cottontail rabbit, listed by Hale (1949) as approximately 9 months. Watson and Tyndale-Biscoe (1953) list the time of fusion of the tibial epiphysis of the European rabbit as averaging 10 months and ranging from 8 to 11 months.

TABLE 1.—*Weights of jack rabbits from the Gray Lodge Waterfowl Management Area, California*

AGE CLASS	SEX	NUMBER	RANGE (gm.)	MEAN (gm.)	STANDARD ERROR
1	♂	60	905–2670	1840	
	♀	48	825–2830	2066	
2	♂	59	1855–2860	2339	
	♀	55	1800–3185	2700	
3	♂	36	2110–2800	2466	32.7
	♀	35	2300–3320	2781	41.8

The faint line showing at the place of epiphyseal closure on the two captives killed at 11 months of age may indicate that the pattern of bony trabeculae was about complete at that time and that the line was about to disappear. It does not seem unreasonable, therefore, to assume that this line, the last sign of growth of the humerus, may disappear at approxi-

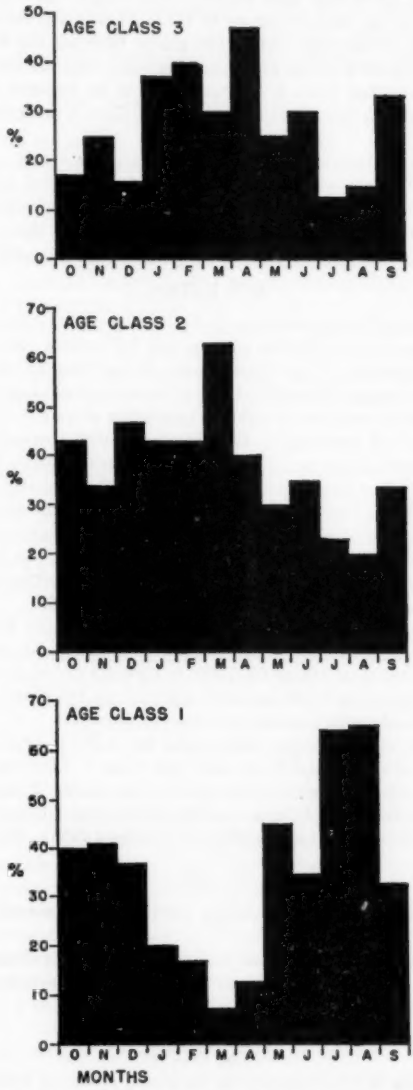

FIG. 3.—Age classes in the kill sample expressed as a per cent of the monthly kill.

mately one year of age. Examination of the data from the sample of wild jack rabbits gives no indication that epiphyseal closure occurs at a different age than in captive-reared animals and it is assumed that wild and captive animals do not differ significantly in this respect.

In the following discussion, those hares listed as Age Class 1 are considered to be from 2 to 9 months of age, but if they have reached adult weight (2100 grams as indicated by the lowest weight of an Age Class 3 animal in Table 1) they are considered to be between 7 and 9 months of age. If they are under 2100 grams, their age can be estimated to within perhaps 2 months by referring to the graph on weight-age relations in Haskell and Reynolds (1947). Those listed as Age Class 2 are considered to be between 10 and 12 months if they have reached adult weight. Those listed as Age Class 3 are considered as older than one year.

The weights of jack rabbits, classified into these three age classes, given in Table 1 add support to this chronology since the weights of some of those listed as Class 1 overlap those listed as Class 3 and thus some of the Class 1 animals are over 8 months of age. On the other hand, the weights of a few listed as Class 2 are less than any for those listed as Class 3 and, thus, these are probably less than 8 months of age even though the epiphyseal groove is closed.

AGE RATIOS

Figure 3 shows the monthly age changes of the killed sample expressed as a percentage of the monthly kill. It can be seen that the summer and fall months (May through December) show the highest proportions of Age Class 1 animals and that by winter these have been reduced to a small percentage of the kill. This confirms the chronology for Age Class 1 as set up above, since this age group seems to shrink in proportion about 6 or 7 months after the early spring and summer peak of breeding. It should be noted that extremely young hares are not represented in this sample as they are quite secretive and not available for collection with the methods used. The smallest hare collected was about 800 grams and thus already approximately two months old. However, animals of this small size are the exception rather than the rule, the majority being about three months or older before they begin to show in the collection.

Age Class 2 reaches its peak of abundance in March at about one year following the first large increment made by early births. Thus it appears that the peak of Age Class 1 animals, as shown in July and August, has by this time passed to Age Class 2.

Age Class 3 reaches its peak percentage in April, one month after the peak of Age Class 2 before the members of February and March litters are old enough to enter into the collection.

The 46 jack rabbits killed on March 23, 1956, in Field 23 included none from Age Class 1 (0 per cent), 25 from Age Class 2 (55 per cent) and 21 from Age Class 3 (45 percent). These figures agree rather closely with expectations based on Fig. 3.

The annual averages of the monthly percentages for each age class are: 35 per cent Age Class 1, 38 per cent Age Class 2 and 27 per cent Age Class 3. Thus, on a yearly average, less than one-third of the collected population is over one year of age. From these average figures a rough estimate of the life span of the jack rabbits in this population can be made, using the original formula of Burkitt (1926) as modified by Petrides (1951). This formula is:

$$L = \frac{1}{f} = \frac{1}{0.73} = 1.37 \text{ years}$$

where L = average longevity of those which survive until they reach the end of the first year, and

f = per cent of young (under one year of age) in the population.

Petrides also gives the following formula for estimating population turnover from percentages of age classes present:

$$T = \frac{\text{Log } 0.005}{\text{Log } (1-f)} + 1$$

where T = the number of years required for the young produced during a certain year to be reduced to 0.5 per cent of their original numbers.

Using this formula with the average data presented above indicates that this population could be expected to turn over in approximately 5.0 years. However, many assumptions had to be made in arriving at these data and it must be remembered that the answers can be nothing but rough approximations. Since the collection methods are biased to collect animals over three months of age, the *L* and *T* calculated here are probably too high. In the absence of more suitable data, it is thought that these figures may at least be suggestive of the dynamics involved in this population of hares. Data from live-trapping and investigations of mortality in this population suggest a rather rapid turnover rate (Lechleitner, 1956).

REPRODUCTION

Male.—The reproductive system of the male jack rabbit is similar to that of the male domestic rabbit. The seminal vesicle, vesicular gland, prostate, paraprostates and bulbo-urethral glands appear identical in gross morphology and histology to those described for the latter species by Bern and Krichesky (1943).

The penis is cylindrical and under ordinary circumstances drawn within the body. The penes of all animals in Age Classes 2 and 3 and of the more sexually mature animals of Age Class 1 can be readily everted by grasping the tips with forceps and pulling gently. Those of Age Classes 2 and 3 vary in stretched length from about 3.5 to 5 cm. It is almost impossible to evert the penes of the younger Age Class 1 animals. It appears that there is an increase in rugosity of the penis with advancing age and many of those on older animals of Age Class 3 have rough bumps or "warts." These were never noted on penes of animals in Age Classes 1 and 2. This "warty" appearance of the penis is helpful for recognizing older males when captured alive.

In embryos near term the testes have already descended into the lower abdominal cavity and cause distinctive bumps in the almost naked skin on either side of the urogenital opening. The inguinal canals apparently remain patent throughout life and it is difficult to be certain if the testes are abdominal or scrotal, for under excitement or shock the hares draw them back into the body cavity. Under most conditions where the testes are large (over 8 cc.) and scrotal, the large epididymides can be easily detected by touch in the upper portion of the scrotum even if the testes themselves have been pulled back into the body cavity.

The scrotum is covered with hair and difficult to distinguish unless distended by large testes. On many of the animals of Age Class 2 and most of the animals in Age Class 3 the scrotal sac develops a rather dark blue color which makes it distinctive. This blue color is apparently retained in older animals even when the testes have regressed to a much smaller size and may no longer lie in the scrotum. The dark blue scrotal sac is an almost perfect indicator of an older animal (Age Class 2 or 3) but its absence does not necessarily mean that the animal is in Age Class 1, for some of the older animals apparently do not develop this color to any great extent.

Figure 4 shows the monthly variation of testicular volume and the presence or absence of spermatozoa in the testes and/or epididymides. Within the year there is a definite but slight cycle of testicular size and production of spermatozoa, even among the adult animals. However, this cycle is not clear-cut and at no time does production of spermatozoa and testicular growth cease for the entire population or for any age class within the population.

The data for Age Classes 2 and 3 indicate that the testicular cycles of these two age groups follow a similar pattern throughout the year. The pattern for Age Class 1 is greatly complicated because young males are entering the population during almost every month and the testicular volumes here shown are from animals ranging in age from about 2 to 9 months.

Within Age Classes 2 and 3 there appears to be a yearly cycle of testicular activity beginning in late November and reaching its peak by January. The peak of activity is more or less maintained through June, but by late July a testicular regression begins in the majority of the animals. During the months of July through November, adult male jack rabbits may be encountered in which testis size is greatly reduced and production of spermatozoa may have

ceased. It appears that when the testes have regressed below a volume of about 4 cc. there is no longer any sperm production. Those animals in Age Classes 2 and 3 (Fig. 3) with testicular volumes below 4 cc. are animals in which spermatozoa are present in the epididymides and not in the testes. Thus it appears that the spermatozoa may be retained for some time in the epididymides after the testes have ceased to produce them. During these months many adult male jack rabbits have a much regressed epididymis, seminal vesicle and vesicular gland, and although spermatozoa are present their numbers are few. It is doubted that these animals are

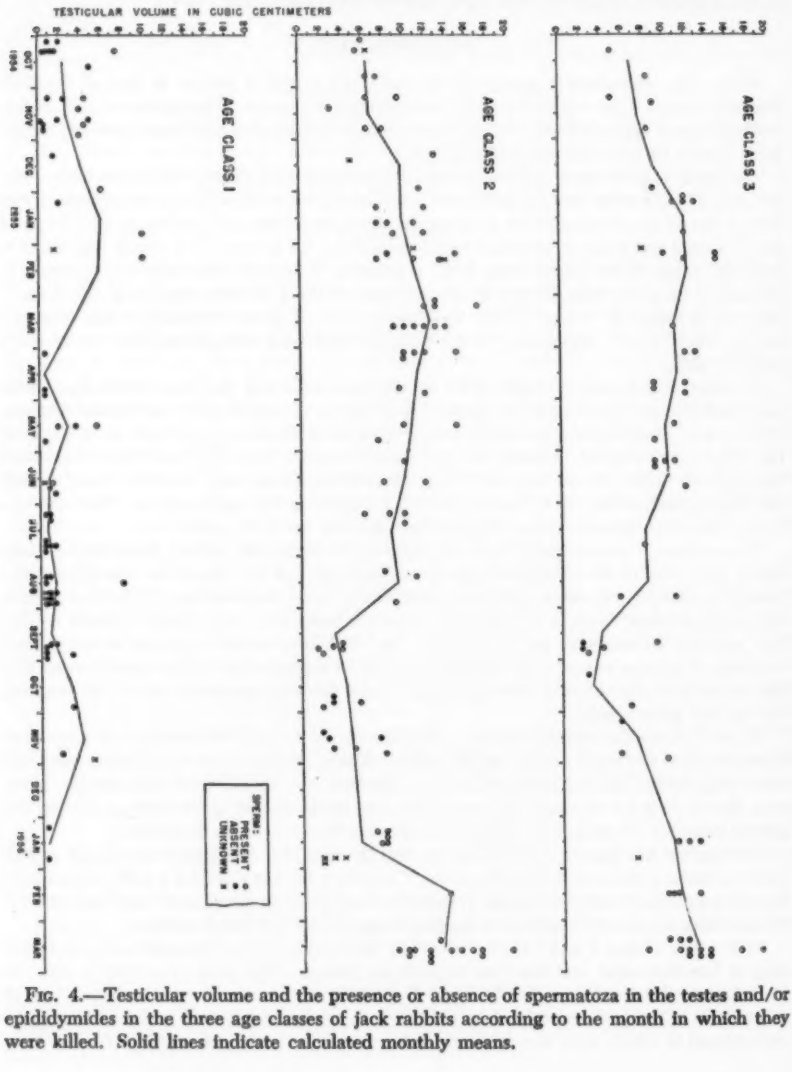

FIG. 4.—Testicular volume and the presence or absence of spermatoza in the testes and/or epididymides in the three age classes of jack rabbits according to the month in which they were killed. Solid lines indicate calculated monthly means.

capable of breeding. It should be emphasized that during any month of the year there are males in any age class which are apparently in full breeding condition as indicated by the size of the testes, large numbers of spermatozoa in the epididymides and fully distended seminal vesicles.

It appears that young jack rabbits in this population are capable of producing spermatozoa at approximately 1900 grams body weight (between 5 and 7 months of age). However, the age at which they become capable of breeding is perhaps greater, for none of the animals in this group had an abundance of spermatoza or fully distended seminal vesicles. These latter conditions were not fulfilled until the animals were close to adult body weight of 2100 grams. Animals born in late summer or early fall reach this weight during a time when breeding activity is high in the population, whereas those born in winter and spring reach this weight at a time when general breeding activity is low. It appears that the former are more likely to become sexually mature at an earlier age than are the latter, since the majority of the subadult weight animals showing large numbers of spermatozoa are found during months of increasing and peak sexually activity in the other two age classes.

The general pattern seems to be one of the onset of sperm production and general reproductive ability at the time the hares reach full body weight (7 to 8 months). This activity may be retained by some individuals with only minor periods of lessened activity throughout the year, while with others there may be a decided seasonal loss of fertility in the late summer and early fall months.

Female.—The reproductive system of the female black-tailed jack rabbit is similar in gross morphology to that of the female domestic rabbit. The main difference between the two lies in the corpora lutea which in jack rabbits may grow to be 12 mm. in diameter whereas those of the domestic rabbit seldom exceed 5 mm. As a result of the development of corpora lutea, the ovaries of jack rabbits vary in size according to the reproductive state. This variation in ovarian size may be expressed as an index using the product of the width times the length of the ovary. These indices were computed on the basis of millimeter measurements. The following mean indices were obtained: non-parous, non-pregnant females, 52.3 $\pm$ 3.52; non-pregnant, parous females, 98.9 $\pm$ 7.94; pregnant females, 239.6 $\pm$ 6.04.

The uterus also varies in size according to the reproductive state. After parturition the uterus quickly shrinks, approaching the diameter of that of a non-pregnant, non-parous animal, even though a new pregnancy ensues. This cycle is repeated with each pregnancy, but if no pregnancy occurs the uterus shrinks and remains small. Once the uterus becomes enlarged, and even before it reaches maximum size, it develops a series of longitudinal stripes or "striations." These striations are retained even though the uterus shrinks almost to its juvenile size and permit the differentiation of animals which have been pregnant from those which have never been pregnant.

The vagina is a single tube leading from the outside to the cervix, and has on its ventral surface near the opening a rather large clitoris. No measurements of the clitoris were taken but it becomes larger as the animal approaches its first estrus and then retains this "adult" size throughout life. The vaginal epithelium, as shown by smears, does not change appreciably with the changes in the reproductive condition of the female. These smears show a preponderance of leucocytes with scattered epithelial cells regardless of the reproductive condition. The color of the vulva is quite variable, ranging from almost completely blanched to dark purple. There appears to be no way of determining the reproductive state of the jack rabbit from the color or condition of the vulva.

The ovary of a young, sexually immature jack rabbit is mostly interstitial tissue with a few small (less than 0.5 mm. diameter) follicles scattered near the surface. As the animal approaches puberty some of these follicles enlarge and reach a maximum diameter of between 1.5 and 2.0 mm. at the first estrus. Some of these larger follicles may rupture and give rise to corpora lutea. The rupture sites appear at first as small volcano-like pits on the surface of the ovary, but by the last stages of gestation they may appear as only clear reddish areas on the

surface. During gestation the corpora lutea increase rapidly in size to a maximum diameter of about 12 mm., the exact size they attain seeming to depend on the numbers present. The corpora lutea may or may not project from the surface of the ovary and it is necessary to slice the ovary to see all of them.

Throughout gestation the corpora lutea in a fresh ovary have a pink color which makes them conspicuous. If another ovulation occurs at the termination of the pregnancy, the new corpora lutea begin to develop immediately and the old lose their red color and become yellow. This change in color apparently occurs almost instantly, for no case was found of a post-partum old corpus luteum being red. By the time the embryos have implanted (7 days in the domestic rabbit) the two sets of corpora lutea approach each other in size. The old corpora lutea usually remain distinct throughout the new pregnancy, but sometimes they are crowded aside by the new ones and are difficult to detect or to measure.

The changes in size of the two sets of corpora lutea, in animals which have apparently experienced a post-partum pregnancy, are illustrated in Fig. 5. Corpora lutea indicated here are the largest of any from a set. The sizes of embryos are spaced on the abscissa to approximate days of gestation, but since no known-age embryos were available these can only be considered as approximations. When the embryos have a crown-rump length of between 100 and 130 mm., the measurements are probably not reliable, as it is difficult to take them accurately at this advanced stage. By this time the old corpora lutea have become quite irregular in outline and are also difficult to measure with reliability. Their apparent fluctuation in size during the later stages of pregnancy is due to this measuring error and does not reflect any renewed growth of regressing corpora lutea. The ovaries of non-pregnant, non-parous animals may be distinguished from those of non-pregnant, parous animals by the persistance of the small yellow scars of old corpora lutea in the latter. Comparisons of ovaries

FIG. 5.—Changes in the sizes of corpora lutea according to embryo size.

with scars of corpora lutea and uteri with striations indicate that the scars are reliable in almost all cases.

There appear to be continuous waves of follicles approaching maturity within the ovary. Some of these apparently never rupture and never give rise to corpora lutea but are destined to undergo follicular atrophy. Two types of follicular atrophy are listed for the domestic rabbit by Hammond and Marshall (1925), and both types occur in the jack rabbit ovary. Type I, or absorption atrophy, is typified by an invasion of the antrum by connective tissue. This type seems common in the jack rabbit. Never were such atrophied follicles noted to develop a yellow color, and thus they could not be confused with old regressing corpora lutea. Atrophy Type II is characterized by a large extravasation of blood into the antrum, and the resulting structure is termed a blood follicle. This is readily visible in the ovary because of its dark color. Only one such case of atrophy was seen in over 400 ovaries examined and it is concluded that blood follicles are rare in the ovaries of the black-tailed jack rabbit.

Occasionally there are corpora lutea which do not have a visible rupture site, and when counts are made of rupture sites and corpora lutea the latter are often in excess. Of 106 pregancies, 19 (18 per cent) showed an excess of corpora lutea over rupture sites. Of 298 corpora lutea, 21 (7 per cent) had no visible rupture sites. Apparently there are corpora lutea formed from follicles which do not ovulate. These corpora lutea appear identical in histology with those resulting from follicles which have ovulated, but sometimes they are smaller in size. Thus, without recourse to the rupture sites, one cannot always distinguish them from true corpora lutea. They appear to be analogous to the corpora lutea atretica of the domestic rabbit as described by Brambell (1944) and are so designated throughout the remainder of this paper.

When the numbers of corpora lutea atretica are analyzed according to the stages of pregnancy, they appear to increase in proportion at the time of implantation of the embryos. It may be that some of them are formed at this time, and not at ovulation as in the domestic rabbit. There is also an increase in their proportion during the very late stages of gestation, but this is probably due to a failure to distinguish all rupture points at these dates. The numbers used for these proportions are small (21 total) and further investigation is needed to establish the exact status of corpora lutea atretica in the jack rabbit ovary. In estimating the number of ova shed, it is perhaps more reliable to use as an index the number of rupture sites rather than the number of corpora lutea, since the latter may give an overestimate of about 7 per cent.

The gestation period of the black-tailed jack rabbit ranges from 41 to 47 days with a mean of 43 days (Haskell and Reynolds, 1947). During the present study several individuals were examined which had apparently just given birth and had recently ovulated, indicating a postpartum heat. Thus the time required for the production of subsequent litters need not exceed the gestation period. Although positive evidence is lacking, it appears that this species resembles the domestic rabbit in being an induced ovulator, only ovulating following copulation or other suitable stimulus. It is also assumed that, as in the domestic rabbit, if this ovulation does not result in conception the animal may go into a state of pseudopregnancy which will last about one-half of the normal gestation time. The pseudopregnancy may end in lactation, but the lactation need not necessarily be as extensive as that following true pregnancy and, in fact, there is evidence that at times it may not even occur (Fig. 6). It is entirely possible that animals which have conceived but which have subsequently lost the entire litter will enter a physiological state resembling pseudopregnancy. During the height of the breeding season (January to July) there are animals in each age class which are parous and pregnant but not lactating (Fig. 6). These animals have ovaries which contain rather large yellow corpora lutea from the last pregnancy indicating that it was recent. It may be that these are animals which have lost their entire litter and did not lactate after this loss. It certainly appears that further work with animals of known breeding history is necessary to establish the role of true or functional pseudopregnancy in the reproductive physiology of the jack rabbit.

Ova may escape the ostium on the side where they form and migrate across the body cavity to be picked up by the opposite ostium. One such case was found during this study. A single ovum was shed from the right ovary and the embryo was located in the left uterus. Since the uterus is duplex, each side having its own distinct cervical canal, transmigration of the ovum by this route is impossible, and can only be accomplished by a transperitoneal migration from one ovary to the opposite ostium. Such migration of ova in the European wild rabbit is reported by Allen, Brambell and Mills (1947) to occur in 0.37 per cent of ova affecting 2 per cent of the litters.

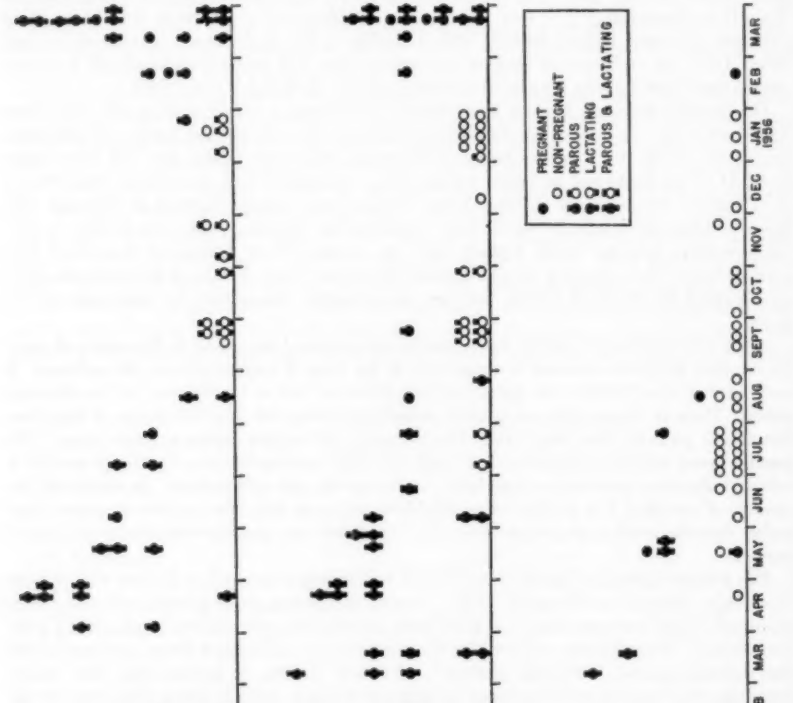

FIG. 6.—Reproductive condition of 213 female jack rabbits in the kill sample by months and age classes.

Usually six nipples are present on the female jack rabbit, two thoracic and four abdominal. The mammary tissue extends as two strips on either side of the midline from the anterior thorax to the perineum. On an animal which is actively suckling young, this tissue may be 13 mm. thick and full of milk, adding considerably to the weight of the animal. The great production of milk is undoubtedly a considerable drain on the physiology of the animal but apparently has little effect on its ability to conceive and carry another litter. In this population it appears the rule, rather than the exception, for females to be pregnant and lactating at the same time. However, the young probably do not nurse throughout the entire period of the new pregnancy. Young jack rabbits in captivity supplemented their suckling with solid food when about ten days of age and when three weeks old had shifted successfully to a dry ration (Haskell and Reynolds, 1947). Thus it may be that in the wild most of the strain of suckling is removed from the female before the new litter is at one-half term.

The female European rabbit permits copulation at all times, even when pregnant or pseudopregnant (Hammond and Marshall, 1925). In the wild this species may copulate frequently during the months just prior to the breeding season (Brambell, 1944). The European hare (*Lepus europaeus*) allows copulation during the later stages of gestation and this may result in a new pregnancy before the old one has run its course, i.e., superfetation (Hediger, 1948; Rieck, 1956). During this study no jack rabbits were found which had ovulated while embryos were present in the uterus, indicating that if superfetation occurs in this population it is very rare.

The presence of spermatozoa in a vaginal smear may be taken as evidence of a recent copulation. Their absence, however, does not indicate that copulation did not occur, since they may be lost for several reasons. During the course of this study vaginal smears were taken from 163 females in all states of reproductive activity and at all seasons of the year. Only three of these smears showed any spermatozoa. One of these was from an animal which was resorbing its single embryo and one was from an animal with embryos in the last quarter of gestation. Spermatozoa were absent even in smears taken from animals which had recently ovulated and in which the uncleaved, or cleaving, ovum was recovered from the oviduct. Several factors may be involved in failure to demonstrate spermatozoa in the vaginal smears. First, they may persist in the vagina for only a short time (perhaps less than 10 hours). Thus smears taken from animals in the afternoon may not show spermatozoa from copulation the previous night. It has long been assumed that copulation in this species occurs at night since it has rarely been seen in the wild (Vorhies and Taylor, 1933). While observing the animals in this study, I witnessed but two completed matings and one unsuccessful attempt. One of those completed occurred near midday and the other in late evening. It seems entirely possible that the majority of matings do occur at night, when observations are difficult to make. Second, post-mortem changes may make it impossible to demonstrate the spermatozoa even though they occurred in the vagina before the animal was killed. Third, the jack rabbit may not copulate as often as does the European rabbit or hare. I am inclined to think that these smears indicate a combination of all three factors. Observations in the field on marked and unmarked hares indicate that female jack rabbits are extremely antagonistic during the breeding season and resent approach by males. It is quite likely that only rarely do they permit copulation at times other than estrus.

Breeding season.—Reproductive data from 213 female jack rabbits killed between October, 1954, and March, 1956, are presented in Fig. 6. For purposes of demonstrating the general breeding season it is perhaps best to confine the discussion to the months from October, 1954, to September, 1955, since the majority of the animals were collected during this period. The weather during this time was typical of the ten-year average for the area. Collections were considerably reduced after October, 1955, except for a last collection at the end of the study. In December, 1956, incessant rain flooded much of the study area.

It can be seen from the graph that there may be pregnant females in this population during any month of the year. However, it was not until January that they appeared in large num-

bers. During this month all of the Age Class 3 females collected were pregnant, several of them for the first time. It appears that these latter animals lived through one complete breeding season without becoming pregnant. By February, all of the females collected were pregnant and this condition persisted until April, when the young of early pregnancies began to show in the collection. By July, there appeared non-pregnant Age Class 2 and 3 animals, but these were not present in large numbers until early September. Thus the general breeding season seems to extend from late January through August with sporadic breeding during any month of the year. The presence of non-pregnant lactating females in July suggests that the general pattern of 100 per cent breeding may be breaking as early as this.

One of the most striking phenomena associated with the yearly cycle of breeding is the change in the number of embryos per female (Fig. 6). In January, the average number is one; it then rises gradually, reaching a peak of almost four by April, after which it gradually diminishes to about one in August. The cycle seems identical in each of the age classes, indicating that age or previous breeding history of the mother is not a contributing factor. At first it was thought that this change may have been due to improving nutrition with the development of the vegetation in the spring. However, a similar change in litter size has been indicated for jack rabbits (Haskell and Reynolds, 1947) and snowshoe hares (Severaid, 1942) kept in captivity and presumably under constant nutritional levels. Vorhies and Taylor (1933) reported similar changes for Arizona jack rabbits, and Kolozov (1941) and Rieck (1956) for the European hare.

The possibility of seasonal changes in size of the litter should be taken into consideration when calculating over-all litter sizes for populations of mammals with extended breeding seasons. Such estimates should not be made unless the entire breeding season is represented and unless the proportions of collections made in the various months are considered. In this study the collections were so distributed that calculation of the yearly litter size by either method gives a similar figure. Thus, if calculated by dividing the total number of embryos by the number of litters, one arrives at a figure of 2.5 young per litter; when the proportions of the collection in each month are considered, this only changes to 2.3 young per litter.

PRENATAL MORTALITY

While examining the jack rabbits it was noticed that some embryos were autolysing *in situ* and that counts of rupture sites and implantation sites did not always agree. Thus it became evident that a number of the ova shed were lost before birth.

Gross estimates of prenatal mortality are sometimes obtained by a simple comparison of the numbers of corpora lutea (or rupture sites) and surviving embryos. Allen, Brambell and Mills (1947) indicate that in the European wild rabbit the prenatal mortality suffered before implantation and that suffered after implantation are distributed independently, and an animal which has suffered one type of loss is no more or less likely to suffer the other type of loss. Brambell (1948) presents convincing evidence that the data for these two types of loss are subject to different limitations and that it is necessary to separate them before a critical analysis can be made. Since these limitations are so admirably set forth by Brambell it is unnecessary to repeat them here. In the following sections the data will be treated with them in mind and, where applicable, as the data for the European rabbit were treated by Brambell.

For 85 pregnancies in this study on which there are sufficient data a comparison of rupture sites and embryos reveals a loss of about 13 per cent of the ova. However, as indicated above, such an estimate is probably far from correct and very misleading. When these data are analyzed with a consideration of when the losses occur, a much greater mortality is indicated.

Pre-implantational mortality involves a loss of ova between the time of ovulation and the time of implantation. In 85 jack rabbit pregnancies a total of 223 ova shed produced 208 implantation sites, indicating a loss of 15 ova (6.7 per cent) in litters in which some ova survived to implant. This loss affected 13 (15.3 per cent) of 85 litters with 11 (12.9 per cent) of these showing a loss of a single ovum and 2 (2.4 per cent) showing a loss of two ova. There

is no indication that such losses are related to the number of ova shed or to the age of the mother; however, the numbers involved here are small and do not permit of critical analysis as do the data of Brambell.

The estimation of the loss of entire litters before implantation almost requires that the living ova or developing embryos be recovered from the tracts before they implant. Because of the inexperience of the investigator at the beginning of this study, it was not possible to recover these with the precision necessary for analysis. However, there remains one other means of estimating at least a minimum loss of entire litters before implantation in the jack rabbit. By using the pattern of increasing size of the corpora lutea following ovulation, as shown in Fig. 5, one can estimate the approximate stage of development of the early embryo. Referring to this figure, it can be seen that in all pre-implantational stages but one the new corpora lutea have not yet reached a size greater than 4 mm. The one exception is twice this size and still the embryos are not visible. It is assumed that this represents the loss of all of the ova sometime before implantation. Thus a minimum of one out of 24 litters (4.16 per cent) which are not yet implanted appears to have been lost entirely. However, if we assume that animals which lose the entire litter will go into a state of functional pseudopregnancy which will last about 21 days, then this one animal represents only about 2.1 per cent of the animals ovulating, since the chances of encountering such a large corpus luteum would be twice as great as that of encountering the smaller corpora lutea of animals which have not yet implanted healthy embryos (7 days).

These figures indicate that 97.9 per cent of the litters survive until implantation and, in these, 6.7 per cent of the ova are lost. Thus the total loss of ova before implantation in litters that survive until implantation and in litters that do not is 8.6 per cent.

A crude estimate of the losses after implantation can be made by comparing the number of implantation sites with the number of healthy embryos. In this study, 93 pregnancies show 12 litters (12.9 per cent) with post-implantation loss and 14 of 233 (6.2 per cent) of the implantation sites show losses. Without critical analysis one might assume that this is the total loss occurring after implantation but, as Brambell (1948) states, such an assumption is far from correct. He has shown, for example, that the loss after implantation is not falling on the embryos as units, since the proportion of embryos showing loss in larger litters is less than would be expected if this were the case. Table 2 presents the percentage of resorbing embryos and the percentage of litters containing them for four different stages in gestation. It is assumed that these stages are of about equal duration. The percentage of abnormal embryos is highest in the second group, falls to a low in the next group, and then rises again in the last group. These data, although few, compare favorably with those of Corner (1923) for pigs and of Brambell (1948) for the European rabbit. All three studies indicate that there is a loss of entire litters sometime before midpregnancy and that these litters being lost drop out of the samples of later stages of gestation. It is possible that the fall in proportion of litters showing loss after midpregnancy in Table 2 may also be due to losses by abortion or because of a failure on my part to distinguish rupture sites at these late stages. Probably all three factors were operating.

TABLE 2.—*Percentages of litters and embryos suffering loss according to the stage of the pregnancy*

STAGE OF PREGNANCY	LITTERS	EMBRYOS	LITTERS SUFFERING LOSS (%)	EMBRYOS LOST (%)
Bump	10	25	10.0	8.3
2–40 mm. C-R	31	87	29.0	11.4
40–90 mm. C-R	17	38	5.8	2.6
90 mm.–term	27	58	7.4	3.4

Brambell (1948) presents several methods for estimating the loss of entire litters after implantation, but only the one based on the relative frequency with which early and late stages of pregnancy are encountered appears applicable to my data. In using this method, it is assumed that the sample is unbiased in that it represents the various stages of pregnancy in the proportions in which they occur in the population and, further, that an embryo of 40 mm. crown-rump length is at about one-half term or 21 days of gestation. Granted these assumptions, then the relative frequency with which hares in early and late stages of gestation occur may be calculated by comparing the frequency with which litters with embryos up to 40 mm. crown-rump length are obtained to the frequency with which litters with larger embryos are obtained. In the present sample there are only 60.6 animals in the late stages for every 100 in the early stages. The difference between the two (39.4 per cent) represents an approximation of the litters which implant and are lost as units sometime before midpregnancy.

The loss of embryos in those litters approaching term is perhaps an approximation of the post-implantational losses in those litters which survive to term. By referring to Table 2 it can be seen that the loss of embryos in litters in the last stages of gestation is 3.4 per cent.

The whole of the loss of ova can be estimated by converting all of the figures given previously into terms of ova shed. Thus 41.5 per cent of the litters appear to be lost entirely and of these 2.1 per cent are lost before implantation and 39.4 per cent are lost after implantation. About 5.9 per cent of the ova are lost in litters that survive and of these 3.9 per cent are lost before implantation and 2.0 per cent are lost after implantation. The total loss of all ova ovulated is approximately 47.4 per cent.

Table 3 compares the losses as estimated in this study for the black-tailed jack rabbit with minimal estimates of losses for the European wild rabbit in England as determined by Brambell (1948). The similarity of the two can readily be seen and it is evident that estimates of prenatal mortality made by comparing the total number of ovulations to the total number of healthy embryos for an entire sample, as is done in column one, are misleading.

TABLE 3.—*Comparison of the prenatal mortality of the black-tailed jack rabbit as determined in this study with that of the European wild rabbit as determined by Brambell (1948). See text for further explanation.*

SPECIES	LOSS ESTIMATED BY COMPARING OVULATIONS TO HEALTHY EMBRYOS FOR THE WHOLE SAMPLE (%)	LOSS ESTIMATED WHEN THE STAGE AT WHICH THE LOSS OCCURS IS CONSIDERED (%)				
		Pre-implantational loss		Post-implantational loss		Total loss
		Entire litter	Ova in surviving litters	Entire litter	Ova in surviving litters	
Jack Rabbit	13	2.1	3.9	39.4	2.0	47.4
European Rabbit	16	1.0	7.0	34.7	0.6	43.3

TOTAL PRODUCTION OF YOUNG

The amount of prenatal mortality should be considered when estimates are made of the total production possible in this population. Litter sizes should be calculated only from healthy embryos in late stages of development to take into account the loss of embryos as units. Especially important is a consideration of the loss of entire litters and the time required for their loss and subsequent return of the female to active breeding.

If all of the litters conceived were successful, then the number of litters produced during any season by a continuously breeding female could be expressed by:

$$N_s = \frac{L}{G}$$

where N_s = number of litters produced during the season,
L = length of the breeding season in days, and
G = length of the gestation period in days.

Applying the data from this study to this formula, we see that:

$$N_s = \frac{242}{42} = 5.75 \text{ litters per season.}$$

Then, multiplying by the average number of young per litter (2.3) we see that the total possible production of a continuously breeding female during the 8-month breeding season is 13.2 young.

However, indications are that approximately 41 per cent of the litters conceived may be subsequently lost in their entirety and that an animal which loses its complete litter is probably removed from further breeding for one-half of the normal gestation period. If we let the proportion of litters lost entirely equal a, then:

Na = the number of actually unsuccessful pregnancies and
$N(1-a)$ = the number of actually successful pregnancies.

Since the time required for Na is $\frac{1}{2}G$ and the time required for $N(1-a)$ is G, then:

$$(\tfrac{1}{2}G)Na + GN(1-a) = L \text{ (length of the breeding season).}$$

Consequently, N (number of litters successful or not) equals:

$$\frac{2L}{G(2-a)}$$

and N_s (number of successful litters) equals:

$$\frac{2L}{G} \times \frac{1-a}{2-a}$$

Using this formula and the data from the present study, the number of successful litters which a jack rabbit in the Gray Lodge population may have if it breeds continuously throughout the main breeding season of 8 months can be calculated as follows:

$$N_s = \frac{2 \times 242}{42} \times \frac{1-0.41}{2-0.41} = 4.27 \text{ litters/female/season}$$

Multiplying by the average number of young per successful litter (2.3) we get a total of 9.8 young produced by such a female. Thus it can be seen that disregarding the proportion of litters lost as units in this population would cause one to assume a seasonal production of young per female about three too high.

DISCUSSION OF THE BREEDING SEASON

The data for both males and females in this population indicate a breeding season extending from January through August, with sporadic breeding occuring at all times of the year. The factors affecting the onset and maintenence of breeding seem to be related to the annual cycle of rainfall and the subsequent greenness of the vegetation. Light appears to play little or no role. A population of jack rabbits in Lake County, California, which is exposed to approximately the same amounts of light but a different rainfall pattern, has a rather limited breeding season corresponding to the nutritional aspects of the vegetation (R. D. Taber, personal communication). Arizona jack rabbits appear to have two peaks of breeding activity which correspond to the two rain periods in that area (Vorhies and Taylor, 1933). The timing of the breeding season of the European wild rabbit in various parts of the world suggests that nutrition, rather than light, may be the regulating factor in that species (Watson, 1954).

The reasons for the apparent loss of reproductive activity by some adult jack rabbits in this population and its maintenence by others are not clear. It could perhaps be an effect

of irrigation, and the fact that many places on the study area, such as ditch banks and sloughs remain green throughout the year. The hares apparently have rather well-defined home ranges. It is possible that an animal might live within an area where there is a decided seasonal alternation in the availability of green food, whereas another not far distant might spend its life along a ditch or slough where seasonal changes are less pronounced.

The breeding season was seriously affected by heavy rains in December, January and February of 1955–56, when whole fields on the study area were inundated and the hares were forced up onto roads and levees and into unflooded fields. Under these crowded, wet circumstances many of them died and many others were in poor condition. Although the breeding season was delayed until about the middle of February, the litter size of hares collected in March after the population had recovered was about the same as that in the previous March when no delay of reproductive activity had occurred.

SUMMARY

At the Gray Lodge Waterfowl Management Area, Butte County, California, 435 black-tailed jack rabbits were collected and examined over an 18-month period.

Differences in the pelves of the hares may be used to tell the sex of carcasses found in the field. The pubic bone tends to be broader and relatively shorter in the female than in the male.

The sex ratio was 198 males to 191 females. The prenatal sex ratio was 26 males to 25 females. Mortality seems to be equally divided between the sexes.

According to the degree of closure of the proximal epiphysis of the humerus, the distribution of age classes in the sample was 35 per cent 2 to 9 months old, 38 per cent 7 to 12 months old, and 27 per cent over one year old, indicating a population turnover within about five years.

The reproductive system of the male jack rabbit is similar to that of the domestic rabbit. In the Gray Lodge population there is a yearly cycle of testicular growth and production of spermatozoa reaching and maintaining a peak from January until late July. Sexually active males are present in all months.

The reproductive system of the female resembles that of the domestic rabbit. However, the corpora lutea of a jack rabbit ovary are much larger. There is a post-partum heat, and during the height of the breeding season females which are pregnant and nursing young are the rule rather than the exception. Female jack rabbits do not copulate as frequently as do female European wild rabbits. There is no evidence of superfetation.

Pregnant females were present during every month but did not appear in large numbers until January. By February, all observed females were pregnant and this condition persisted until April when the young of early litters began to appear. Young jack rabbits are apparently capable of breeding by the time they are approximately eight months old. The older female hares maintained 100 per cent breeding activity from January through August. The rainfall pattern and the greening of the vegetation seem to be the main factors associated with the peak of the breeding season. The average number of embryos per female is one in January, four in April and one in August.

If prenatal losses are estimated by comparing the number of ovulations with the number of healthy embryos for the entire sample, it appears that only 13 per cent of the ova are lost, but when the time at which the loss occurs is considered it appears that as high as 47.4 per cent may be lost. If the prenatal mortality in the Gray Lodge population of hares is disregarded, one would overestimate the production of young per female per breeding season.

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BREEDING HABITS OF THE SWAMP RABBIT WITH NOTES ON ITS LIFE HISTORY

By Thomas P. Hunt

Although rabbits have always had a certain number of hunting enthusiasts, their popularity has increased in recent years with the reduction in numbers of other game species. As a result there is need for obtaining information basic to the management of our rabbit populations. This study was undertaken to supply some of that information for the swamp rabbit, *Sylvilagus aquaticus aquaticus* (Bachman), and is condensed from a thesis presented for the Master of Science degree at the Agricultural and Mechanical College of Texas. The study was done under the supervision of Dr. William B. Davis, Professor of Wildlife Management, and Dr. R. O. Berry, Professor of Animal Husbandry.

Two ranches in Brazos County, east-central Texas, containing swamp rabbit habitat were selected for the study. One, the Bonifazi Ranch, comprised 1,000 acres; the other, the McCullough Ranch, about 2,500 acres. Both areas had extensive deciduous woodlands in the creek bottoms tributary to the Navasota River. Strips of upland prairie bordered both these woodlands which contained much the same types of vegetation and had the same general aspect. Both ranchers were encouraging the growth of grasses by girdling and felling trees.

Species characteristic of the crown layer of the deciduous woods were *Quercus nigra* L., *Fraxinus texensis* (Gray), *Planera aquatica* (Walt.), *Celtis occidentalis* L., and *Carya aquatic* Michx.

Species characteristic of the small tree, shrub and vine understory were *Salix nigra* Marsh, *Gleditsia aquatica* Marsh, *Cornus stricta* Lam., *Berchemia scandens* (Hill), *Rubus velox* Bailey, *Ilex decidua* Walt., *Vitis candicans* Engelm., *Smilax glauca* Walt., and S. *bona-nox* L.

Wherever sunlight penetrated the crown layer, and the vines and shrubs did not shade the forest floor, dense growths of grasses, such as *Uniola sessiliflora* Poir., *U. latifolia* Michx., *Axonopus furcatus* Hitchc. and *Arundinaria tecta* (Walt.), were in evidence. The last was found along the banks of ponds and sloughs.

The first collection of rabbits was made February 20, 1954 on the Bonifazi Ranch. Green vegetation was barely apparent and rabbits were easily flushed. By the end of April the foliage in the woods was becoming dense, the rabbits were not starting as far in front of the hound as they had earlier, and the hound was trailing mostly by scent. During late May most of the rabbits were taken in a field of knee-high grass, in which scrub oaks were interspersed at about 20-yard intervals, in an ecotone between the bottomlands and the prairie. Rabbits were not seen in this area in the spring before the grass was high or after it has dried out late in summer. It is believed that a combination of succulent food and adequate cover induced the rabbits to enter this ecotone for short feeding periods.

During July and August, the hottest part of the year, swamp rabbits were difficult to flush. This may have been due in part to the hound's inability to scent and trail easily in hot, dry weather. During this period, swamp rabbits appeared from an hour before sunset to several hours after on the shoulders of a road crossing the bottoms and were easily hunted there at night. A three-man team was found most effective, with one man driving a vehicle, one operating a spotlight from one fender and the third shooting from the other fender.

By late September most of the grasses and vines were brown and withered and the leaves were beginning to fall. The rabbits were no longer feeding among the grasses of the ecotones. Toward the end of November the foliage was almost entirely gone and the rabbits flushed at greater distances from the hound than they had during the summer. Some rabbits whose forms were located in dense underbrush would not flush until the hunter jumped on the cover in which they were hiding.

During late January and early February, 1955, quotas of rabbits were taken with ease. It is true that the collector had increased in skill as a swamp rabbit hunter and that the visibility in the woods had improved. But still another reason was that the new breeding season was underway. This may have caused the rabbits to become less timid. In any event they did not flush as far ahead of the hound as they had during late fall and early winter, although cover was just as sparse.

Two other lagomorphs occupied the study areas—*Lepus californicus,* which was seen only in the arid pastures, and *Sylvilagus floridanus,* which was occasionally found on the periphery of the swamp rabbit's habitat. Cottontails observed during this study always occurred in the ecotone between woods and prairie or on the wooded uplands.

In the course of the investigation, 152 swamp rabbits (see Table 1) were examined. Of this total, 102 were shot as they flushed in front of a hound and 32 were shot at night with the aid of a spotlight.

The presence or absence of sperm in males was determined by cutting the epididymis in two and teasing the halves with a probe. The reproductive state of nongravid females was determined by the condition of the uterus. Does with translucent or white uteri less than 2 mm. in width were classed as virgins. Uteri more than 6 mm. in width with prominent blood vessel were recorded as flaccid. Grayish-hued uteri between 2 mm. and 6 mm. in width were given no designation.

Eighteen swamp rabbits were taken alive when they entered holes in the ground or hollows in trees. These were weighed, measured, and placed in hutches for further observation and for breeding.

Artificial insemination was used in attempting to impregnate the does. This method eliminated the fighting and consequent deaths attendant to natural mating cited by Dice (1929) and Bissonnette (1938) and it also facilitated an accurate determination of the gestation period. Each time an impregnation was attempted, semen was obtained by excising one of the testes of a mature

TABLE 1.—*Age classes and sex ratios, by months, of 152 swamp rabbits from Brazos County, Texas*

MONTH	ADULTS		JUVENILES		TOTALS
	Male	Female	Male	Female	
Feb.	4	3	0	1	8
Mar.	5	8	1	1	15
Apr.	2	5	0	4	11
May	2	6	2	0	10
June	2	0	4	9	15
July	2	3	2	3	10
Aug.	3	4	2	1	10
Sept.	2	3	2	5	12
Oct.	2	4	2	2	10
Nov.	6	5	1	0	12
Dec.	6	2	2	2	12
Jan.	5	7	0	1	13
Feb.	5	8	1	0	14
Totals	46	58	19	29	152
Per cent	30.2	38.1	12.5	19.4	
Total males	65		Total females	87	
Per cent males	42.7		Per cent females	57.2	

buck and mashing the epididymis. The semen thus obtained was mixed with saline solution and used to inseminate two does. Electrical stimulus was first used to obtain semen but the ejaculations contained no sperm. Ovulation in does was induced by injecting gonadotropic hormones into the veins in the ears.

GESTATION PERIOD AND CONDITION OF YOUNG AT BIRTH

Before each captive doe was inseminated she was observed until it was determined that she was not gravid. The shortest period of observation was 36 days. Three of the 9 inseminations resulted in known births. Each of these, except the one attempted on doe No. 30, resulted in the doe having distended teats by at least the 20th day following insemination. Doe No. 30 died 9 days after insemination. Autopsy revealed that she had two ruptured follicles but no uterine swellings.

In speaking of the domestic rabbit of the "Belgian hare type," Hammond and Marshall (1925) state that ovulation occurs 10 hours after coitus. Brambell (1944) reports that domestic rabbits ovulate 12 hours after copulation. The gestation periods reported in the present study were arrived at by counting the number of days from the date of insemination to the estimated time of birth and then subtracting 11 hours to compensate for the time interval between stimulation and ovulation.

Doe No. 24 was inseminated May 3, 1955. When her cage was checked the afternoon of June 11 there was no evidence that a birth had occurred. About 10:00 AM on June 14, a very young, fully furred rabbit, whose eyes were slitted as if they had just started to open, was standing in the cage. During a period of about 10 minutes this young rabbit was seen to walk several feet in the cage using long, wobbly, cat-like strides. That it had been rejected by its mother was shown by its enfeebled condition. It died after an attempt was made to feed it warmed cow's milk with an eye dropper. This young rabbit probably was born the night of June 11, or possibly on the morning of June 12. If so, the gestation period was 39–40 days.

Doe No. 29 was inseminated on January 28, 1955. Her cage and nest box were checked twice each day from the 25th day following insemination to the morning following parturition. At 6:00 PM on March 8 there no young rabbits but at 9:00 AM the following morning one was lying in a corner of the cage. It was furred and its eyes were closed. It was thin and emaciated and although the doe placed herself astride the new-born young, it was not seen to nurse and was found dead at 8:00 AM the following morning. The calculated gestation period was 39–40 days.

On March 19, 1955, doe No. 29 was inseminated again. An X-ray was taken on April 25, 37 days after insemination. The skeletal structures of three embryos were clearly visible. There were no young in this doe's cage during the daylight hours of April 27. At 5:30 PM on April 28, one young rabbit with well-developed pelage and closed eyes was found dead in her nest box. It was born late in the evening of April 27, or early on the morning of April 28. The calculated gestation period was 39 days.

From the preceding accounts it can be seen that the gestation period of the *S. aquaticus* is 39 to 40 days and the young are born with the pelage well-developed and the eyes closed. A comparison of the young born in captivity with those described by Svihla (1929) indicates that the eyes probably open and the young rabbit is able to walk by the second or third day following birth.

REPRODUCTIVE PATTERN

Most of the studies of the reproductive patterns in *Sylvilagus* have been conducted in the northern part of the United States and have indicated relatively short, well-defined breeding seasons. In regions with milder climates there seems to be more diversity. Ingles (1941), in discussing *S. auduboni* in southern California, said that pregnant females, lactating females, and young in the nest have been found in every month of the year except January, July, and October. The breeding season of *S. bachmani* in west-central California was found by Mossman (1955) to extend from December to June inclusive. Majors (1955) said that in Alabama *S. floridanus* begins breeding in January and ends in September.

In east-central Texas, gravid does of *S. aquaticus* were found in each month of the year except September, October, and December. But during each of

these three months at least one doe was taken with flaccid uterus, which probably indicates that she had been pregnant sometime within the preceding 10 days. Although the breeding season in *S. aquaticus* in this part of Texas is nearly year-long, it can be shown that a definite pattern of high and low periods of fertility exist. Of the seven gravid does taken between January 27 and February 2, 1955 only one contained embryos that were considered to be as old as 20 days. The abrupt increase in fertility which occurred about the middle of January is similar to the sudden onset of breeding that Brambell (1944) described in *O. cuniculus* in England. He attributed the lack of fertility before the season started to the males, while Mossman (1955) said males of *S. bachmani* in west-central California were in breeding condition approximately one month before the females. In *S. aquaticus*, a reduction in the quantity of sperm was noticed as early as August in some bucks. Others seemed to contain "adequate" amounts through the fall and winter. The peak of breeding in 1954, as measured by the percentage of gravid does, was reached in February and March. From April through August there seems to have been a leveling off with the exception of June when the drop in percentage of gravid females was due to the large number of juvenile females in the sample.

According to Bissonnette and Csech (1939) sexual activity was advanced in *S. transitionalis* by exposing the rabbits to artificial light. In the Sacramento Valley of California Ingles (1941) found *S. a. auduboni* breeding the year around because the area was irrigated and there was green vegetation throughout the year. Fitch (1947) discovered that breeding in *S. a. vallicola* was limited to late fall, winter and spring when green forage is abundant in the western Sierra Nevada foothills. *S. bachmani* was found to be infertile during the dry period in west-central California, according to Mossman (1955). He also pointed out that a correlation of their breeding cycle with the amount of daylight would have to be inverse to that discovered by Bissonnette and Csech (*op. cit.*).

Although most of Brazos County was extremely dry in 1954, water persisted in parts of the bottomlands during the entire period of the study and some green vegetation was apparent until at least mid-November. The presence of green vegetation in swamp rabbit habitat is probably an important factor in the maintenance of this rabbit's comparatively high level of reproduction through the fall in this area. Another explanation for this late seasonal breeding, not necessarily divorced from nutrition, is that each doe has a limited breeding capacity and that females born early in the season are responsible for the late season breeding (Brambell, 1944). In Alabama, Majors (1955) found indications of a similar pattern. In the present study one gravid doe was taken on June 20. The writer believes this rabbit was born in the same breeding season in which it was killed. It weighed about half of what an adult doe should weigh. Each of the standard measurements except the hindfoot was less than the smallest measurements of all the other gravid does taken during the study. Two embryos were found in the right horn of her uterus and one in the left.

Most of the studies on cottontails revealed sex ratios with a slight preponderance of males. Trippensee (1948) points out that most of these ratios were obtained by trapping during the winter. He reports that 58 per cent of 391 rabbits taken from holes in the ground during the winter in Ohio were females. Gerstell (1937) offered evidence showing that females are more sensitive than males to rigorous weather conditions. The conclusion was drawn by Trippensee (*op. cit.*) that if there is a real difference in the sex ratio of cottontails it probably favors females.

The results of the present study tend to corroborate Trippensee's viewpoint. November and December were the only months in which more bucks than does were taken, but these two months preceded the onset of breeding in January and perhaps the bucks became less timid as this period approached. If the actual sex ratio is equal, or if it favors the males, there appears to have been some factor that caused the females to be taken more frequently during the greater part of the year. One explanation could be that a doe heavy with young does not run as rapidly or take alarm as quickly as an unencumbered buck. Also a doe with nestlings might be slow in leaving the area of her nest. It seems, however, that the preponderance of juvenile females taken in June and in three other months supports the theory that the sex ratio favors the females.

LITTER SIZE

Audubon and Bachman (1846–54) said they had been told that the swamp rabbit has from four to six young per litter. The litters Svihla (1929) examined ranged from one to six, and the embryos ranged from three to five with an average of 3.7. Of the 87 does examined in the present study, 58 were judged to be adults. Twenty-eight of the adult does and one juvenile were gravid. The pre-natal litter size ranged from one to five with an average of 2.83. Two and three embryos were the most frequent, each occurring in 9 does. Embryos that were obviously being resorbed were noted but not used in the calculations. Occasionally small masses were encountered in the uterine folds that could have been advanced resorptions, but because of the difficulty of positive identification they were not recorded.

The average litter sizes recorded for other species of *Sylvilagus*, under somewhat comparable climatic conditions, appear slightly higher than the average found in the present study. Orr (1940) gives 3.6 for *S. auduboni* in California. From western Florida, Blair (1936) reported that four females of the marsh rabbit, *S. palustris*, carried from three to five embryos each. Of females having uterine swellings the litter size was found to average four in *S. bachmani* in California (Mossman, 1955). Both embryos and placental scars were counted by Majors (1955) for an average of 3.1 for *S. floridanus* in Alabama.

The lack of uniformity of opinion as to what should be included in an embryo count casts some doubt on the value of these comparisons. To further complicate matters Brambell (1944) concluded that, in *O. cuniculus* in England, 59 to 63 per cent of all embryos conceived are lost through resorption. If this per-

centage is characteristic of other wild members of the family, even a study in which only perfectly developed embryos were counted would be misleading as to the productivity of the animal.

There seems to have been a positive association between the average litter size by months and the percentage of does that were gravid during those same months. An apparent explanation is that the litter sizes and percentages of pregnant females declined after the rabbits' initial reserves were decreased, and then fell again after the quantity or quality of food grew less as summer advanced. Another possibility is that does born in the same season were doing the late season breeding and because of their age were carrying smaller litters.

PARASITES

Ward (1934) and Smith (1940) identified some of the parasites which infested swamp rabbits in Oklahoma. Erickson (1947) also cites Price (1928) as having identified some of the parasites of this rabbit in Texas. Since Price (*op. cit.*) did not name the species of rabbits from which the parasites were collected, perhaps Erickson had other information on which he based the inclusion of one genus of Trematoda and three genera of Cestoda among the swamp rabbit's parasites.

In the present study all of the rabbits taken were not examined, but from time to time specimens were combed for external parasites. Heavy infestations of a flea, *Hoplopsyllus affinis,* were found throughout the year. Another parasite was the larva of the bot fly, *Cuterebra buccata.* The first rabbit found parasitized by this larva was taken June 4. When these larvae occurred they usually appeared about the necks and groins of younger rabbits. The largest of three larvae, when pulled from the neck of a juvenile, left a hole 10 mm. deep and 7.5 mm. in diameter. Several of the rabbits displayed scars which looked as if they had been caused by this larva.

Specimens of the mite *Psoroptes equi cuniculi* were found in the ears of one swamp rabbit. This mite was also reported by Ward (1934). A different mite *Eutrombicula alfreddugesi,* the common chigger, was first noticed on a swamp rabbit on July 14. As the summer advanced larger colonies of chiggers appeared on the undersides of all the rabbits examined. By the first week in November chiggers were noticeably fewer and shortly thereafter were not found at all.

Ticks began to appear in numbers about the middle of May and disappeared about the end of November. The rabbit tick, *Haemophysalis leporis-palustris,* infested most of the rabbits taken during this period. The lone star tick, *Amblyomma americanum,* was found infrequently in the present study.

Two series of swamp rabbits were examined for helminth parasites. Those found were identified as *Cittotaenia* sp., *Passalurus* sp., *Trichuris* sp., and *Obeliscoides* sp. Both Ward (1934) and Smith (1940) had previously recovered these four genera from swamp rabbits. Blood smears from captive rabbits were examined on two different occasions with negative results.

GENERAL HABITS

When vegetation was sparse and when they were closely pursued by the hound, swamp rabbits occasionally sought refuge in burrows or in hollow trees. Many of the burrows were made by armadillos, *Dasypus novemcinctus,* which were numerous in the study areas.

The nest of *S. aquaticus* has been described by various authors (Strecker and Williams, 1929; Svihla, 1929; Goodpaster and Hoffmeister, 1952). In the present study one unoccupied nest was located. It was about 6 inches in diameter and was a mixture of abdominal fur and dried grass hidden under the edge of a brush pile.

Kennicott (1858) reported this rabbit as usually resting on top of logs, stones, and other elevations. The writer never saw a swamp rabbit on any of the elevations Kennicott (*op. cit.*) described, but fecal pellets were frequently found on top of, and close to, such objects. Both Seton (1928) and Svihla (1929) reported this rabbit using forms. On several occasions in the present study, swamp rabbits reoccupied forms a few feet from the writer and many times they flushed from heaps of brush or dense tangles of vines which on closer inspection proved to contain forms.

The swamp rabbit's affinity for water is well known. Audubon and Bachman (1846–54) said it fed on many aquatic plants. Kennicott (1858) reported it as frequently diving under water and also told of one hiding in water with just its nose breaking the surface. In the present study rabbits were occasionally seen swimming across creeks and ponds or running through shallow bodies of water when being trailed by the hound or run by sight. Although the hound never had any trouble trailing across water and would do so without breaking stride, he once stopped in the middle of a pond apparently puzzled as to which way the trail led. Perhaps this was an instance of the behavior Kennicott (*op. cit.*) described. On one occasion a rabbit was seen to swim across a creek and crawl under some projecting tree roots at the water's edge. It remained there, partly submerged in about five inches of water, until the hound dragged it out.

Two noises were known to have been made by *S. aquaticus* during the course of this study. One of these was the well-known thumping of the ground with the hind feet when the rabbit was first alarmed. The other was a scream often heard when a rabbit was wounded and could not move or was seized by the hound or the observer.

Rabbits were never seen during rainstorms, but they seemed to be very active a day or two after a rain when the ground was not too wet. Part of this impression may be due to better trailing conditions for the hound.

SUMMARY

The reproductive pattern of *Sylvilagus aquaticus* was studied in 152 specimens collected along tributaries of the Navasota River in Brazos County, Texas. At least 10 rabbits were taken each month from January, 1954, to March, 1955. Captive rabbits were used in nine

attempted artificial inseminations which resulted in three known births. This method seems superior to natural mating in accurately determining the gestation period, which was found to be 39 to 40 days. The young are born with the pelage well developed and the eyes closed. There is evidence that the eyes begin to open and the animal is able to walk on about the second or third day.

Gravid does were found in each month of the year except September, October, and December. Other evidence indicates that some breeding occurred during these months. About the middle of January a sudden increase in the percentage of gravid does occurred, with the peak for the year in late February and in March. Of 58 adult does taken, 28, including one immature doe, were gravid. Pre-natal litter size ranged from one to five, averaging 2.83. The average litter size was highest during the peak of the breeding season and was lowest just before the period of least fertility. Two and three embryos were the most frequently recurring litter sizes.

Four genera of helminth and two species of arthropod parasites which had been recorded previously as parasitizing this rabbit were identified. In addition *Eutrombicula alfreddugesi*, the larvae of *Cuterebra buccata*, *Hoplopsyllus affinis*, and *Amblyomma americanum* were recovered for the first time.

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GENETIC, PHYSIOLOGICAL AND BEHAVIORAL BACKGROUND OF REPRODUCTION IN THE RABBIT

V. NONRETRIEVING OF NEONATES

BY SHERMAN ROSS, VICTOR H. DENENBERG, G. P. FROMMER AND P. B. SAWIN

The albino rat has become increasingly and almost exclusively popular in psychological experiments (Beach, 1950; Schneirla, 1946). Other species, such as dogs, cats and sub-human primates, are used infrequently, and rabbits and guinea pigs are relatively ignored. Frequently, results obtained in the rat are generalized to other species, and sometimes to all animals, though perhaps only one subline of the species has been investigated (Munn, 1950; Ross and Smith, 1955).

Recently, we have observed some of the difficulties arising from such generalizations. In the rat the retrieving response of the mother when the young are disturbed or displaced is one of the strongest and most studied elements in maternal behavior (Wiesner and Sheard, 1933; Beach and Jaynes, 1956). It might easily be assumed that this character is common to all laboratory animals. Yet experience for over 30 years by one of us (P.B.S.) has provided little if any reason to suspect any indication of retrieving in the rabbit. Technical assistants with five to nine years of experience likewise can recall no observed cases of retrieving in the colony, although a large proportion of litters in a colony of approximately 300 breeding females are born during working hours. Frequently litters are found scattered on the floor of the cage, but in no case has the mother been observed to move them to the shelter of the nest. Blood stains outside the nest, although the young are within it, are sometimes observed. Such an event may indicate some movement of the young by the mother. However, the stains could be the result of discharge from the mother, who has often been observed

to leave the nest between birth of successive young in a single parturition. Thompson and Worden (1956) reported no evidence of retrieving. Communications from Roscoe F. Cuozzo, George S. Templeton, Harry V. Thompson and W. King Wilson likewise reported no positive evidence of retrieving. Deutsch (1957) has also obtained negative results.

Examination of the literature has revealed only suggestive evidence relating to retrieving in any of the wild relations of the domestic rabbit, viz., Seton (1909) in the English wild rabbit (*Oryctolagus cuniculus*), the black-tailed jack rabbit (*Lepus californicus*) and the European hare (*Lepus europaeus*); Beule and Studholme (1942) in the cottontail (*Sylvilagus floridanus*); and Orr (1942) in the brush rabbit (*Sylvilagus bachmani*). With reference to the carrying phenomenon in the jack rabbit (*Lepus townsendi*), Cahalane (1947: 607) states, "No one knows when they (the young) leave the nest. It is possible that the mother herself distributes them, one in a place, when they are a few days old." Lang (1925) agrees with this but states that rather than being moved by the doe, the already well-developed new born hare follows the mother into the hiding place.

With respect to other species, Causey and Waters (1936) have reviewed the early literature on the carrying of young by mammals and performed preliminary investigations on the rat, dog and cat. For all species in which retrieving is found, this response would seem to serve the same functional needs. It provides for the care of the infants, which are both blind and hairless, and appear to be relatively helpless at birth. Since this description holds for the rabbit, it would seem to follow that their mothers should exhibit a similar maternal behavior pattern. Because the work already done indicates that retrieving, when present, readily lends itself to quantitative evaluation and experimental study, it seemed essential to attempt to determine the existence of this behavior in the rabbit before proceeding further with our program. We are presenting this brief report of our attempts in this connection.

Procedures and results.—The cage and nesting facilities and general pattern of use by the rabbit have been previously described by Sawin and Crary (1953) and by Ross *et al.* (1956). Variations in time of building and quality and location of nest have been described by Sawin and Curran (1952).

A simple apparatus was designed to measure retrieving. It consisted of an alleyway 2 feet wide, 9 feet long and 16 inches high, constructed in such a way that it could be attached to any nest box, and placed so that it was well illuminated during the experimental test.

The testing pattern was basically the same throughout, although the particular form was varied. At the beginning of each test the nest box, containing the mother and young, was removed from the home cage in which the young were born and connected to the alleyway. The test consisted of removing the young from the nest box and distributing them in the alleyway. Following this placement, the mother's reactions were observed and recorded. This procedure was started a few hours after birth and continued at intervals for a few days.

Initially, the young were placed at the far end of the runway and the mother left in the box. If the mother made no move to leave the nest box, several of the young were placed nearer to her, and/or she was then placed on the alley next to the young. Later, in view of the apparent absence of retrieving, the apparatus was abandoned and the tests were carried on in the home environment. Here the young were merely removed from the nest to the floor of the cage, and the mother was not disturbed in any way. In certain cases intervention by the observer was necessary because of attacks on the young either by the mother or by a rabbit in a neighboring cage.

Nine does of mixed ancestry were tested in this manner for 2–5 daily trials of not less than 7 minutes each. Two mothers were kept under observation for a minimum of 30 minutes, one mother for 2 hours. In all, 24 trials were made. The trials were limited to short periods to avoid any possibility of chilling the young.

In no case was any effort made on the part of the doe to move the young. The different females showed varying degrees of interest in the young, ranging from a lack of interest to the extent of standing on the young despite their vocalized protests, through simple sniffing and nosing of the young, to active and solicitous maternal attention, including careful and extensive licking. The young of one doe were observed attempting to nurse while in the test situation out of the nest box. The doe's reactions to the experimenter's handling of the young ranged from no interest, through curious approach, to foot stamping, vocal objection and threats of active attack (Sawin and Curran, 1952).

Observation of mothers in the experimental situation and also in the home cage environment lead us to believe that retrieving is not a usual part of the normal behavioral pattern of the rabbit in the colony as maintained. There are several possible explanations for the apparent absence of this behavior in this species.

Discussion.—One possibility is that the relatively barren environment in which these rabbits are raised may inhibit retrieving. Riess (1954) has reported that female albino rats reared in an environment in which the animals had no opportunity to manipulate or carry objects did not build nests nor retrieve the young. Riess also reported an unpublished study by Birch in which it was found that female rats prevented from licking their genital regions until parturition did not attempt to lick, clean or suckle the newborn animals. The environment of the rabbits in this colony, however, is not as barren as that just described. The environment is perhaps closer to that of conventionally reared rats. This hypothesis also does not account for the failure to find retrieving in wild rabbits and hares who presumably live in a much richer environment than do laboratory-reared animals.

Although the environment in which these rabbits are reared probably does not inhibit retrieving, it may not act to facilitate this response. It may be possible to elicit retrieving behavior by raising rabbits in an environment in which they are forced to manipulate and carry objects in order to survive. Though

this would be an experimentally produced situation, it would give some insight into the experiential factors necessary to evoke this response. If such findings were obtained, it would help explain why more indirect evidence of retrieving is reported for wild as compared to domestic rabbits. The wild animals would presumably engage in more manipulation than domestic rabbits.

Another hypothesis is that maternal behavior, at least the retrieving aspect, has been in some way minimized in achieving the maximum adaptation of the rabbit to its environment. The maternal patterns of the domestic rabbit are relatively simple. Ordinarily, nursing is rarely observed. Some mothers display varying degrees of timidity and interest in the young or in aggression toward the attendant or other intruder (Sawin and Curran, 1952; Denenberg *et al.*, 1957), whereas others are unconcerned with the manipulation of their young. Other than this, there appears to be little interaction between mother and young, so characteristic of many other species, except for the limited feeding periods.

This is not unlike the pattern which exists in wild rabbits and hares. According to Beule and Studholme (1942), "Nestling cottontails usually received little maternal care, as no female was ever known to remain with her nestlings except at feeding periods." Although the females apparently made daily visits to the nests, adult cottontails were seldom observed in the vicinity. Some exceptions were reported in which the female maintained a close watch over the nest, and Trippensee was quoted as having observed defense of young in response to their screams, which is not unlike the aggressive protection noted by Sawin and Curran (1952). Seton (1909) stated that in general cottontails feed the young only at night and do not approach the nest by day. Ingles (1941) reported that while a person was in an observation blind 12 feet from a cottontail nest, the mother was never observed. Studies of tracks in sawdust placed about the nest indicated visits for nursing which were carried on apparently by simply crouching over the nest. By this method Ingles found gaps between feeding as long as 31.5 hours. Cahalane (1947) stated that in both the cottontail and the jack rabbit the females do not stay with the young but remain some distance away. Only at night do the females return to the nest to nurse the young.

If these various observations and descriptions present a true picture of the maternal behavior in the species studied, we may conclude that this pattern is simpler than in many other species. A possible interpretation of this greater simplicity may be made in terms of the adaptation of these species to their environment. The rabbit and the hare are dependent on their freezing, fleeing and dodging abilities and, if necessary, will aggressively fight for survival. The female rabbit, tied down to helpless, highly dependent young requiring much care and attention, would seem to be at a disadvantage.

The young of the rabbit and the hare are remarkable in their independence from maternal care, even though quite helpless at birth. They are able to go for long periods of time without feeding, as noted above. Ingles (1941) has ob-

served that slight pressure on the top of the cottontail rabbit's nest elicited vigorous reaching movements by the young animals. The longer the interval between feedings, the stronger the response. He suggested that this is a nursing response to the mother as she crouches over the nest to feed them.

This phenomenon may be observed in the domestic rabbit. The newborn rabbit also has well-developed motor abilities. One neonate was observed to crawl the length of the 9-foot runway. Two-day-old rabbits have been observed to lift themselves up a 30° incline into their nest. Orr (1942) reported that young brush rabbits returned to the nest if removed and placed with their noses to the nest fur. A similar response over a greater distance may be observed in the young of domestic rabbits. It is most easily seen between 7 and 14 days of age, but has been observed in neonates less than 24 hours old. These motor responses appear to be controlled by temperature differentials for the young will stop creeping if they find a sheltered place.

The above observations and interpretations are a first attempt to deal with the absence of the retrieving response in the rabbit in terms of its behavioral pattern. In view of the apparently complete absence of this reaction in the rabbit in the 24 test trials, it seems worthwhile to bring them to the attention of other workers in this field and to point out the problem in trying to generalize from one species to another even though there may be close relationship.

SUMMARY

Nine newly parturient domestic rabbits of mixed ancestry were tested for retrieving behavior under a variety of conditions. No retrieving of the young was observed. Maternal attention toward the young ranged from no concern to solicitous licking. A review of the literature, largely from the naturalists' writings, provided no convincing evidence that retrieving behavior was common among wild lagomorphs, although several authors believed in its existence. Tentative interpretations of the absence of this behavior were made in terms of the rabbits' particular adaptation to its environment and the neonates' general independence from extensive maternal care.

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ANTLER ANOMALIES OF MULE DEER

By W. Leslie Robinette and Dale A. Jones

In this paper we describe a few antler anomalies observed primarily among mule deer (*Odocoileus hemionus* ssp.). Six previously unpublished records of mule deer bucks lacking one or both antlers are given. A number of cases of antler deformities seemingly associated with old body injuries are discussed, as are a few cases of antlered does and antler retention by bucks.

Most antler abnormalities which we have observed among bucks seem to fall into two classes according to origin: those of genetic origin and those of traumatic origin.

Antler abnormalities of genetic origin.—In bucks lacking one or both antlers, the defect is apparently of hereditary origin since all of the affected animals have come from one small drainage, the Oak Creek area of central Utah

embracing about 33,000 acres. Also the testes, for those bucks where gross observations were made by the hunters and in two cases by the writers, were of normal size and presumably would have been functional during the breeding season.

Robinette and Gashwiler (1955) have previously reported a few mule deer bucks from the Oak Creek area that lacked one or both antlers. Since publication of this paper, six added specimens, making a total of 14, have been observed by the senior author within the same area. A brief description of each of the six recent cases is given below.

A 4-year-old buck, killed October 26, 1954, by Tharel Larsen of Delta, Utah, had no left antler and only a 3¾-inch-long club-like antler on the right. Apparently injured early in growth, the antler had grown ventrally beside the deer's head and the velvet on the medial side had not been rubbed off. The antler measured 1.1 inches in diameter 1 inch from the end, compared to only 0.4 inch for the pedicel. The antler lacked a burr and merged indefinably into the pedicel. On the left side of the skull was a tiny pedunculated bony structure—about ¼ inch in diameter and in height—directly opposite the antler. There was also a low bony prominence at the angle formed by the frontal with the parietal bones on the left side. This buck was a large mature animal, which hog-dressed 182 pounds, showed some neck swelling and, according to the hunter, possessed normal sized testes. This buck was nearly identical to one described earlier by Robinette and Gashwiler (*op. cit.*, Plate I). The two bucks were killed within one-half mile of each other.

Another one-antlered buck was killed in the Oak Creek area, October 29, 1955, by Ennes Alldredge of Ogden, Utah. This buck, antlerless on the right side, possessed a massive 7-point antler on the left side (Plate I). The antler was 1.5 inches in diameter 1 inch above the burr and 25½ inches in length along the outside curve. A pedunculated bony protuberance about ½ inch in height and diameter was present on the right side. This buck was about 8 years old, weighed 204 pounds hog-dressed, displayed a swollen neck and, according to the hunter, possessed normal sized testes.

The year-old skeleton of an antlerless yearling buck was found by the senior writer April 14, 1955, on the winter range of the Oak Creek area. The deer, known to have been a buck from the still attached dried-up penis, was believed to have been 20–21 months of age at death. It possessed a tiny ½-inch pedicel on the right side—the same size as that of many fawns found dead during winter—and examination of the tip showed there had been no antler growth the preceding fall. The left side was smooth at the normal pedicel site.

On October 30, 1956, the senior writer found a large antlerless buck fatally wounded and not recovered by the hunter within the Oak Creek area. The buck had small rounded bony protuberances, less than ½ inch in height, on each side, but possessed no antlers whatsoever. The deer was about 4 years of age and would probably have hog-dressed close to 200 pounds. He possessed such masculine features as an enlarged neck, a conspicuously white muzzle

and normal sized testes. Weight of the testes (73 grams) indicated the buck was approaching breeding condition. Furthermore, histological sections of the testes made by Roger deRoos revealed sperm in the seminiferous tubules.

Another deer hunter, when shown the head of the above animal, stated that he too had killed a large antlerless buck within the Oak Creek area sometime during the early 1940's.

An antlerless mule deer buck, which weighed 161 pounds hog-dressed, was killed within the Oak Creek area during the 1957 deer hunt. There was only the slightest suggestion of pedicels, tiny bumps rising but ⅛ inch above the surface of the skull. The buck's neck showed some enlargement, his face was nearly white, and his testes were of normal size for a mature animal, measuring 6.6 by 3.6 cm.

A male fawn weighing 48 pounds, hog-dressed, and which had no trace of antler pedicels, was killed during the 1957 hunt in the Oak Creek drainage. It is probable that this fawn, had he reached maturity, would also have been antlerless.

A skull anomaly which we found in three of the bucks lacking one or both antlers adds support to the belief that the antlerless or semiantlerless condition in bucks from this one area may have a genetic basis. The defect was noted in the postorbital arch where normally in deer the supraorbital process of the frontal and the temporal process of the malar bones join to form a solid arch, but in these three bucks the processes showed a distinct hiatus from 0.1 to 0.4 inch (Plate II). The defect was found both on the left and right arches of each animal, substantiating the belief that this too was of hereditary origin. The defect has been noted in one doe, also from the Oak Creek area. After noticing the anomaly, we examined 89 skulls of mule deer bucks and 50 of does, many from outside the Oak Creek area, and found no additional cases.

Antler abnormalities of traumatic origin.—Our interest in the subject of antler growth as influenced by body injuries has stemmed from having observed several bucks so afflicted and also from statements in the literature. Rörig (1901) believed that injuries to the bones and soft tissues of the extremities of deer were often responsible for diminished and deformed growth of their antlers, and that the degree of antler deformation paralleled the severity of the injury. He believed, also, that injury to a front leg resulted in changes in both antlers, although greater in the one on the affected side, whereas injury to a hind leg invariably resulted in deformation of the contralateral antler. Wislocki (1952) agrees that extensive injuries to the skeleton might conceivably interfere with metabolic processes involved in bone deposition and hence affect antler growth. However, he feels there is no basis whatsoever for the belief that injury to a hind leg will influence growth of the antler on the opposite side.

Clarke (1916) believed that severe body injuries may cause the antlers to become deformed. He further stated that the malformed antler was nearly always on the same side as the injury. He listed only two examples out of a

total of six, however, in support of the latter contention. Clarke also stated that if the animal had been injured on both sides of the body, both antlers would be deformed; he cited one example. The remaining three cases were of deer

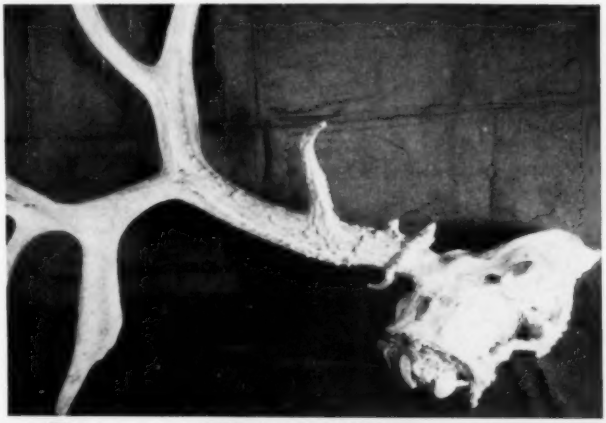

PLATE I

TOP: Skull of a one-antlered buck killed in central Utah. The tiny rudimentary right pedicel indicates that there never was an antler on that side. LOWER LEFT: Skull of an antlerless mature buck showing a hiatus in the right postorbital arch. The left arch is similarly affected. LOWER RIGHT: Head of buck from which the lower right hind leg was missing from the tarsal joint through an old injury. The contralateral antler is conspicuously deformed.

PLATE II

TOP: Buck with old injury to the elbow joint of the right front leg and with deformity to the left antler. BOTTOM: The left front leg of this buck is missing from just below the carpus through an old injury. Both antlers are deformed although the right one seems less so. A 1-inch point arises directly from the pedicel whereas the main beam extends caudad for about 3 inches before turning dorsad.

each with a malformed antler and a body injury but it was not stated which side of the body was afflicted.

Dixon (1934) recognized no connection between a malformed antler and a body injury but he gave a photograph (Fig. 43) of an old buck with an injured left hip, a normal 4-point antler on the right and a spike on the left. In this case, the deformed antler and body injury were on the same side. Moore (1931) noted many cases of antler abnormality in cervids seemingly associated with worn down or missing molars on the same side as the antler abnormality.

Penrose (1924) removed the right testis from one mature Sika deer (*Cervus nippon*) and the left one from another. Antler growth in subsequent seasons was smaller in both animals but the one having the right testis removed had a left antler that was deformed or had fewer points than its companion for the subsequent three seasons. The other buck, however, showed no difference in the right and left antler although both were smaller than prior to unilateral gonadectomy. Jaczewski (1952) unilaterally castrated two red deer (*Cervus elaphus*) stags and three roebucks (*Capreolus capreolus*) of different ages and found that symmetry of the antlers in subsequent seasons was not influenced. Darling (1937) stated that if a stag were injured on one side of the body, antler growth the following year would be defective on the opposite side, but he listed no specific cases.

Our observations of the influence of body injuries upon antler growth of mule deer indicate a correlation between the two phenomena. We have, however, records of antler deformities in deer in which no serious body injuries were found and also records of deer with conspicuous body injuries but normal antlers (Table 1). In some cases antler deformation probably resulted from a

TABLE 1.—*Mule deer bucks with old body injuries but no antler deformities**†

CASE NO.	LOCATION AND NATURE OF OLD INJURY	STATUS OF BUCK	AGE	OBSERVER	DATE	PLACE
1	Injury to right front leg	live	mature	Drobnick	June 23 '54	Oak Cr., Ut.
2	Metatarsal injury of right leg	dead	?	Murchie	?	South Ida.
3	Left tarsus injury; hooves long through nonuse	dead	?	Thompson	Oct. 1949	Northeast Ut.
4	Young fawn with leg broken 3" above tarsus was ear-tagged; killed next year but no external evidence of old injury	dead	1-yr.	Robinette	Oct. 1951	Oak Cr., Ut.
5	Injury to right carpus	dead	2-yr.	Robinette	Oct. 1955	Oak Cr., Ut.
6	Toes of left front foot missing	dead	2-yr.	Robinette	Oct. 1955	Oak Cr., Ut.
7	Flesh wound—left hind leg	dead	mature	Julander	Oct. 1954	Monroe Mt., Ut.
8	Flesh wound—left hind leg	dead	2-yr.	Isom	Oct. 1957	Midway, Ut.

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† Gilbert and Hill (1956) recorded the case of an elk with an old tarsus injury and normal appearing antlers, although the antlers were asymmetrical—one having three points, the other five.

TABLE 2.—*Deer and elk having an old body injury and deformity of one or both antlers**

CASE NO.	DESCRIPTION OF BODY INJURY	ANTLER DESCRIPTION (R=RIGHT; L=LEFT)	STATUS OF ANIMAL	AGE	OBSERVER	DATE	PLACE
			Deer:				
1	Left hind foot off below tarsus	L-normal; R-3″ shorter, fewer points and twisted	dead	mature	Spackman	Sept. 1956	Blue Mt., Ut.
2	Right hind foot off at tarsus	R-normal 4-pt.; L-abnormal (Pl. 1)	dead	mature	Day	Nov. 3, 1956	Trail Mt., Ut.
3	Enlargement of left tarsus	L-normal 4-pt.; R-earlength with numerous small points	dead	mature	Jones	Sept. 24, 1955	Henry Mts., Ut.
4	Right hind leg non-functional, held out behind	R-normal; L-smaller and conspicuously deformed	live	mature	Robinette	Sept. 30, 1952	Duck Cr., Nev.
5	Right elbow rigid and enlarged (Pl. II)	R-normal; L-deformed	dead	2-yr.	Robinette	Oct. 1954	Oak Cr., Ut.
6	Left humerus enlarged through old injury	Antlers normal length but twisted and atypical in form	dead	2-yr.	Johnson	Oct. 1955	Millard County, Ut.
7	One front leg crippled	One antler normal, other deformed	dead	?	Johnson	1940's	Canyon Mts., Ut.
8	Old flesh wound 5″ above left tarsus	Antlers same length; L-normal; R-flat towards upper portion from which three 1.5-inch pts. arose	dead	?	Rensel	Nov. 1955	Nash Draw, Ut.
9	Right front leg off below "knee"	R-normal 3-pt.; L-6″ long and curved down beside head	dead	?	Bown	Oct. 1955	Fish Lake, Ut.
10	Left hind leg drawn-up from flesh wound	R-normal 3-pt.; L-4″ high with many small basal points	dead	?	Bown	Oct. 1955	Central, Ut.
11	Left front leg off at carpus	L-normal 4-pt.; R-7″ long, 2-pt., had grown up then back	dead	mature	Bown	Oct. 1955	LeVan, Ut.

12	Left front leg off 2" below carpus (Pl. II)	Both atypical but L perhaps more so than R	dead	6-yr.	Robinette	Oct. 20, 1956	Oak Cr., Ut.
13	Left hind leg off just below tarsus	L-normal 3-pt.; R-10", twisted spike	dead	?	Spackman	Oct. 1956	Beaver, Ut.
14	Left hind leg drawn-up but nature of injury undetermined	L-normal 2-pt.; R-twisted 4- or 5-inch spike	live	probably 2-yr.	Robinette	Aug. 27, 1956	Oak Cr., Ut.
15	Deer ran with crippled gait but limb involved not determined	R-normal 5-pt.; L-2/3rds as long with 3 pts. jutting up and a 4th down besides eye	live	mature	Robinette	Nov. 19, 1955	Mescalero Res., New Mex.
16	Bulge in right mandible	R-9-inch spike; L-5-inch spike	dead	1-yr.	Robinette	Oct. 22, 1955	Oak Cr., Ut.
17	3.5-inch bulge in right front leg above carpus	Both conspicuously deformed	dead	4-yr.	Robinette	Oct. 1957	Oak Cr., Ut.
18	Old injury to left shoulder	L-normal 4-pt.; R-4" long and curled	dead	?	Jones	1940's	Siskiyou County, Calif.
19	Buck limped from injury to right hind foot just above hooves	R-normal 3-pt.; L-3" long jutting outwardly	live	probably 2-yr.	Robinette	Aug. 27, 1957	Oak Cr., Ut.
			Elk:				
1	Right hind leg crooked from enlarged tarsus	R-normal; L-smaller and of abnormal shape	dead	?	Spackman	Oct. 1956	Northeast Ut.
2	Conspicuous bulge on one of right ribs	R-normal 5-pt.; L-shorter and grown down by eye	dead	?	Bown	Nov. 1951	Mt. Nebo, Ut.

* Acknowledgment is due the following individuals for observations used in this table: Dean Spackman, Douglas Day, and Casey Bown of the Utah State Fish and Game Department and Austin Johnson of the U.S. Fish and Wildlife Service.

direct injury during early growth. On the other hand, some old body injuries may go undetected unless conspicuous, as a misshapen limb.

Injuries like the one mentioned by Clarke (*op. cit.*), in which a buck had three broken ribs, could be overlooked in an animal which had not yet been skinned. Casey Bown of the Utah State Fish and Game Department killed a bull elk (*Cervus canadensis*) having an abnormal left antler and an old rib injury on the right (Table 2, elk, case 2). This injury might easily have gone unnoticed. We encountered a case in which a body injury would have gone unnoticed had the buck not been ear-tagged (No. 4015) (Table 2, deer, case 16). Because it was of known age, the head was kept and in the process of cleaning its skull an old injury to the right mandible was noticed. The spike antler on the opposite side was 5.1 inches long compared to one 9.1 inches long on the right side. We cannot be sure that the difference in antler size was associated with the mandible injury, but we suspect it was.

Our limited observations indicate that conspicuous antler deformities among deer having undetected body injuries make up a very small percentage compared to the proportion of crippled deer having antler deformities. Thus, for a sample of 618 bucks, lacking old conspicuous body injuries, examined at the Oak Creek checking station in 1955, 1956 and 1957, there were only 13 (2.1 per cent) with deformation of one or both antlers to the degree noted among deer with conspicuous old body injuries. Excluded, however, are those animals which for genetic reasons lacked one or both antlers, discussed earlier, and the so-called "cactus" bucks discussed more fully in a later section. One of the aforementioned 13, however, was buck No. 4015 in which subsequent cleaning of the skull revealed an injury to the mandible. Undetected body injuries may have been present on some of the remaining 12 deer but, in most, abnormality probably resulted from injury to the antler during early growth or possibly to a diseased condition of the pedicel as suggested by Cowan (1936). Observations by the writers and associates show that 23 buck deer and 1 bull elk with old conspicuous limb injuries have shown 17 (71 per cent) with a conspicuous deformity of one (14) or both (3) antlers. Three additional observations were not included because these could not be considered as obvious cases of body injury. Only search for such evidence after initial observation of antler deformity disclosed these injuries. The figure of 71 per cent is a high incidence of antler deformity compared to that found among bucks lacking conspicuous body injuries (2.1 per cent).

Table 2 shows that nine animals were known to have had an injury to the front part of the body. In six of the nine, the antler on the side opposite the injury was deformed, whereas in the three remaining instances both antlers were deformed. However, in two of the three cases, the antler on the side of the injury exhibited a greater deformity. Nine animals listed in Table 1 had a hind leg injury and all exhibited a contralateral antler deformity as did the elk having an old rib injury.

Our observations agree with Rörig's (*op. cit.*) in that an injury to a hind leg seems to affect antler growth on the opposite side, but agree only in part with his observations of an injury to a front leg. Rörig reports in such instances that both antlers are affected although more extensively on the injured side. The latter condition was true in two of nine cases which we observed, but in the other instance where both antlers were deformed the degree of deformity appeared the same, while in the remaining six instances only the antler on the side opposite the injury was affected.

Rörig's and our observations, that the deformed antler is on the side opposite the hind leg injury, are not verified by the single case quoted from Dixon (*op. cit.*) nor by a single case listed by Clarke (*op. cit.*). It appears the number of observations are too few to draw definite conclusions regarding which antler will be deformed in relation to the injury. However, we do believe the incidence of antler deformity is too great in animals with old body injuries to attribute the association to mere chance or to simultaneous occurrence of antler and body injury. We believe that most body injuries noted in the deer and elk described by us resulted from gunshot wounds and if so the injuries were incurred at some season prior to one in which deformed antlers were grown. Belief that limb injuries are largely caused by gunshot wounds is substantiated by our observations of 3,328 live fawns, 3 to 4 months old, in Utah and eastern Nevada before the hunting season. We noted but two crippled fawns among them, an incidence of 0.06 per cent, while observations after the hunting season revealed nine cripples among 2,954 fawns for an incidence of 0.31 per cent, or a five-fold increase. It is conceivable that a buck could accidentally break a leg during the early stages of antler growth and injure an antler at the same time, but we suspect this could explain only a small proportion of the cases. There appears to be no obvious physiological reason, however, why deformation should affect one antler so much more than both.

Permanent antler retention by bucks.—Permanent retention of antlers in the velvet is an anomaly occasionally encountered in cervids. These animals are known in Utah as "cactus" bucks and are probably deficient in production of androgens. Wislocki (1943) discussed the factors controlling antler-gonad periodicity and pointed out that the testicular hormone is responsible for hardening of the antlers in summer and probably for the shedding of the velvet in the fall. It is also known that castration during the early life of the deer will permanently inhibit the development of antlers, but castration in later life will result in the development of persistent antlers in the velvet. Conceivably, accidental gonadectomy could occur in wild deer, but it is more likely that atrophy of the androgenic elements is responsible for the condition of persistent velvet.

Hunters killing "cactus" bucks commonly report them as being castrates. While this possibility has been recognized above, we suspect in most instances the hunters have overlooked atrophied testes. We have examined but three "cactus" bucks reported by hunters as castrates in which the scrota were still

TABLE 3.—*Antlered does observed by authors and associates in Utah*•

CASE NO.	ANTLER DESCRIPTION (R=RIGHT; L=LEFT)	EVIDENCE OF FERTILITY	STATUS OF DOE	AGE	OBSERVER	DATE	PLACE
1	R-nothing; L-pedicel 1¼" but no antler growth	Pregnant with twin fetuses	dead	mature	Robinette	Mar. 11, 1948	Manning Cr., Ut.
2	R-pedicel ¾", antler ¾" in velvet but no burr; L-protuberance ¼"	Lactating according to hunter; doe's poor condition serve to confirm statement	dead	3-yr.	Robinette	Sept. 22, 1956	Antimony, Ut.
3	Both 3- to 4-inch spikes, no velvet	Observed for 1 hr. with a fawn; ribs showed and muzzle not white as in a buck	live	mature	Robinette	Oct. 14, 1955	Oak Cr., Ut.
4	Both 8-inch spikes in velvet	Lactating, followed by twin fawns when shot, according to hunter	dead	old	Smith	Oct. 23, 1949	Ephraim, Ut.
5	In velvet; R-10-inch spike; L-4 pts. from burr	Lactating, followed by twin fawns when shot, according to hunter	dead	mature	Leonard	Oct. 1941	Sigurd, Ut.
6	Both 9-inch spikes in velvet	Milk in udder attached to carcass	dead	mature	Antrei	Oct. 18, 1941	Mayfield, Ut.

• Observations of the following individuals have been used in this table: Justin Smith and the late Boyd Leonard of the U.S. Forest Service and Albert Antrei, high school science teacher, Manti, Utah.

attached to the carcasses. Atrophied testes were found in each case. Dr. Ward Huffman, formerly of the Bureau of Animal Industry, examined a "cactus" buck killed on the Kaibab National Forest and also found atrophied testes. The senior author saw a mature "cactus" buck at the Kanosh, Utah, deer-checking station in 1943 and the hunter stated it had very small testes.

The causes of testicular atrophy in deer are not well understood. Brucellosis, when localized in the testes of domestic cattle, is known to result in infertility following subsidence of the inflammation (Manthei *et al.*, 1956). Brucellosis has been reported in deer and elk but apparently is very rare (Honess and Winter, 1956). By the same token, "cactus" bucks appear to be very rare, at least in Utah. In a sample of 5,522 bucks observed at checking stations in central Utah, we noted but six "cactus" bucks. Clark (1953), however, reported them as being fairly common in the Tucson Mountains of Arizona.

Lloyd Stevens, District Game Manager of the Utah State Fish and Game Department, castrated two mule deer bucks, ages about 8 and 20 months, in February, 1956. Both bucks were killed the subsequent October. Antlers of each animal were normal in size, form and number of points, but they had failed to fully harden and still retained the velvet.

Antlered does.—Instances of antlered does, killed by hunters, are often recounted in newspaper articles but we have obtained few detailed accounts of such animals. We have been unable to procure the reproductive tracts from any antlered does but the notes we have taken on antler growth, etc., have been recorded in Table 3.

SUMMARY

Six mule deer bucks are described in which one or both antlers were missing. All of these came from the Oak Creek area of central Utah; together with eight previously described bucks, this makes a total of 14 such animals observed from this relatively small drainage. An associated genetic defect noted in three of these bucks was a hiatus between the supraorbital process of the frontal and the temporal process of the malar bones. Normally, in deer, these processes fuse to form a continuous bony arch.

Nineteen buck deer and two bull elk having an old body injury and a deformity of one or both antlers are described. The incidence of a conspicuous deformity of one or both antlers among deer with old conspicuous body injuries seems too high to ascribe the association to chance or to a concurrent injury to both the body and the growing antlers. Thus, for a sample of 618 bucks without conspicuous body injuries, only 13 or 2.1 per cent with a conspicuous antler deformity were noted. Contrasted with this was an incidence of 71 per cent with antler deformity among 23 buck deer and one bull elk possessing conspicuous body injuries. In 21 cases of deer and elk afflicted with both antler deformity and an old body injury, deformity was restricted to a single antler in 18. In 16 of the 18 cases, records were obtained for the location of both the abnormal antler and the injury, and in every case the injury and the deformed antler were contralateral to one another. Some exceptions to this condition were noted in the literature, however.

A brief discussion of "cactus" bucks and of six does with antlers or pedicels is given.

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BREEDING RECORDS OF CAPTIVE WHITE-TAILED DEER IN ALABAMA

BY ARNOLD O. HAUGEN

Published records on breeding and gestation periods of white-tailed deer, *Odocoileus virginianus*, are few. Records in the Southeast are nonexistent. Such information, however, has been published in limited amounts for the northern race by Brown (1936), Cheatum and Morton (1942, 1946), Haugen and Davenport (1950) and Taylor (1956).

TABLE 1.—*Source and subspecies of deer, Odocoileus virginianus, used in breeding studies*

NUMBER	SEX	SOURCE	SUBSPECIES
3002	♀	SW Alabama	*osceola*
3004	♀	Choccolocco Area NE Alabama	Probably mostly *virginianus*
3014	♀	SW Alabama	*osceola*
3026	♀	Out of 3004 and 3005	At least one-half *osceola*
3005	♂	SW Alabama	*osceola*

The secretive nature of deer makes it very difficult to collect information on breeding in the wild. Confinement of several whitetails at the Alabama Cooperative Wildlife Research Unit for a 6-year period, beginning in 1950, has made it possible to gather data on rutting season activity, gestation and fawning. The deer used in the experiments were all taken from wild stock in Alabama. Buck 3005 and does 3002 and 3014 came from southwestern Alabama where no restocking has been done and, therefore, they are regarded as *Odocoileus virginianus osceola.* Doe 3004 came from the Choccolocco Game Management Area in the northeastern part of Alabama which was stocked with Pisgah, North Carolina, deer in 1938–41. The ancestry of this doe is questionable since the native deer at Pisgah had been mixed with deer stocked from Florida, the coast of North Carolina and New York (Ruff, 1939). Her ancestry was at least 8 years removed from the latest stocking in the Choccolocco Area. The size of this deer is similar to that of other deer in the Southeast. The color of her coat, however, is a little darker. The ancestry of doe 3026, which was raised in captivity, is indicated in Table 1.

The deer were kept in concrete-floored pens, the smallest of which measured 8 × 9.5 ft. and the largest 12 × 24 ft. The diet of the deer was inadequate during a period starting in 1951 to April, 1952, when does 3002, 3003 and 3004 and buck 3005 were used in experiments to determine the effect of ammate-treated foliage (Haugen, 1953) and in other dietary experiments. When not on such restricted one-species diets, they were given rations of 9 per cent protein mule feed and a poor quality hay. After May, 1952, they were provided a diet of 18 per cent protein dairy feed and good quality alfalfa hay. Some scratch grain or corn, cottonseed meal and mineralized salt were provided from time to time. The diet was more than adequate during the period when fawns were produced.

TABLE 2.—*Period during which buck had daily access to does for breeding*

BREEDING SEASON	DATES
1951–1952	October 25–March 9
1952–1953	December 4–March 15
1953–1954	December 21–March 21
1954–1955	December 21–February 27
1955–1956	December 21–March 11
1956–1957	January 3–March 8

The buck each fall was dehorned as soon as he started shedding his velvet. This was done for the safety of both the caretakers and the does. The antlers were cut off about one-half inch above the burr (Haugen, 1957). During the periods indicated in Table 2, the buck was put with the does for about 15 minutes each day. At first he was put with each doe separately; however, this procedure was subsequently abandoned in favor of putting him into a pen with all the does at one time. This was done because it was found he was not confused by numbers and went about his function of breeding just as effectively in a "harem." The buck was watched constantly while in the pen.

Mating behavior.—Copulation with the doe in heat was evidenced by a final lunge by the buck which usually knocked the doe to her front knees or rammed her entirely off her front feet. Additional circumstantial evidence of ejaculation was the quick flashing spread of the white "disk" hair on the buck's buttocks. The spreading of the white buttock hair was almost too quick to be seen. Successful contact was evidenced in the doe by the temporary hump left in her back following contact. The exact time of the first service was recorded. The doe usually refused to stand for the buck following two successful contacts in a period of about 15 minutes. When separated from the doe in heat, by means of a series of doors operated from outside the pen, the buck usually became very belligerent, charging and raking the fence with his head.

Not one of the mature does used in these experiments allowed the buck to mount except on the day she was in heat. In fact, most of the time the older does seemed afraid and frequently ran from him in great excitement. One old doe, however, often refused to give ground and fought him off with her front feet. On the day a doe came into heat, however, her nature changed completely and she then stood quietly and calmly until serviced one or two times, after which she usually avoided further contact by walking away when he tried remounting. On the day following mating, neither the buck nor doe was attracted to the other, and in no case did she allow copulation on the following day. On some days when none of the does would stand for him, he became belligerent and butted them severely, especially so when he was about 2½ to 3½ years old. Had he not been dehorned, he would have severely injured or killed the captive does. A similar belligerency on the part of the buck when a doe refused to stand for him was reported by Severinghaus (1955).

During the breeding season the buck commonly urinated on the tarsal glands on the inside of the hocks of his hind legs by bringing the hocks close together, then leaning his body weight backward until the hind legs were brought directly under the sheath of his penis so that the urine ran onto the hocks and glands. The real purpose of this behavior in the wild is not known. Is it to mark territory to warn other bucks to stay away, or is it to add "irresistible" lure to does, or both?

Breeding season.—Records were obtained of 17 successful matings by the penned deer. These occurred between December 26 and February 21 (Table 3). Ten of these matings occurred in the last eight days of January. The single late

TABLE 3.—*Breeding, fawning and gestation data for whitetails in Alabama*

DOE NO.	DATE BRED	FAWNED	GESTATION IN DAYS	AGE AT FAWNING, YEARS	PARTURITION NUMBER	NUMBER FAWNS
3002	2/3/53	8/15/53	192.8	4	1st	1♂
3002	1/29/54	8/8/54	191.2	5	2nd	2♀
3002	1/25/55	8/7/55	193.9	6	3rd	1♀, 1♂
3002	1/23/56	8/5/56[1]	195.0	7	4th	1♀, 1♂
3002	1/27/57[2]					
3003	1/28/52[3]					
3004	2/21/53[3]	9/8/53	198.2	4	1st	1♀
3004	1/6/54	7/19/54	193.5	5	2nd	2♂
3004	12/26/54	7/11/55	197.2	6	3rd	2♂
3004	12/31/55	7/13/56[1]	195.9	7	4th	2♂
3004	1/29/57[4]					
3026[5]	1/24/55	8/8/55	193.9	2	1st	2♀
3026	1/27/56	8/4/56[1]	190.0	3	2nd	2♂
3026	1/8/57[3]					
3014	2/12/54	8/28/54	196.5	2	1st	1♂
3014	1/28/55	8/3/55	186.9	3	2nd	1♀
3014	1/24/56[3]					

[1] Leap year. One day added for gestation period.
[2] Sacrificed before fawning time.
[3] Also services 1/28/53.
[4] Probably missed earlier heat period (started breeding experiment 1/3/57).
[5] Mixed ancestry. Half SW Alabama, half Pisgah ancestry.

record of a successful mating, on February 21, involved a doe (3004) that had been unsuccessfully serviced on January 28, 21 days earlier. Apparently she conceived at the time of her second estrus. The period of recurring heat as reported for northern whitetails by Cheatum and Morton (1942) was 28 to 29 days.

An attempt to breed three fawns at six months of age was unsuccessful. Two of the fawn does did not breed even when administered dosages of 2 mg. E.C.P. (estradiol cyclopentyl-propionate) in an attempt of force ovulation. A retreatment of the same two fawns eight days later (February 8) with 10 mg. Stilbestrogen (diethylstilbestrol alpha estrodiol dipropionate) also failed. The drugs were administered by Dr. Walter J. Gibbons of the Alabama Polytechnic Institute School of Veterinary Medicine.

Fawning.—Twelve fawning dates were recorded with the earliest fawn dropped on July 11 and the latest on September 8. Six of 12 known fawning dates occurred between August 3 and 8. Of the remaining six births, three occurred before and three after this period. These birth records fall within the limits of the fawning period as reported by Lueth (1956) who estimated the season from computed ages of yearling deer killed in the hunting season.

The gestation period as determined from 12 pregnancies was 193.8 days, with a minimum of 187 and a maximum of 198 days. This average is roughly

TABLE 4.—*Measurements of fawns (in inches) at birth*[1]

DOE NO.	AGE OF DOE AT FAWNING, YEARS	SEX OF FAWN	WEIGHT, LBS.	TAIL LENGTH	EAR LENGTH	HINDFOOT LENGTH	TOTAL LENGTH	SHOULDER HEIGHT	SINGLE OR TWINS	FAWN NO.
3002	4	♂	5.7	3.8	3.2		24.4	14.8	S	3007
3002	5	♀	5.1	3.9	3.0	8.2	23.0	14.5	T-1	3008
		♀	5.3	3.8	2.8	8.5	24.6	14.5	T-1	3010
3002	6	♂	5.8	3.6	3.0	8.5			T-2	3023
		♀	5.8	4.0	3.2	8.7			T-2	3030
3002	7	♂	6.4	4.6	3.2	9.2	24.2	15.0	T-3	3028
		♀	6.1	4.6	3.0	9.1	24.5	15.5	T-3	3029
3004	4	♀	6.6	4.0	3.4	9.4	25.1	15.2	S	3026
3004	5	♂	5.8	4.5	3.1	9.5	24.1	15.0	T-4	3009
		♂	6.4	3.9	2.8	9.0	25.5	15.2	T-4	3016
3004	6	♂	7.4						T-5	3019
		♂	6.8						T-5	3020
3004	7	♂	6.4	4.5	3.1	9.4	24.8	15.5	T-6	3027
		♂	5.9	4.5	3.2	9.2	24.0	14.0	T-6	2152
3004	8									
3014	2	♂	5.4	4.2	3.2	9.1	24.0	15.5	S	3018
3014	3	♀	5.5	4.0	2.9	8.5	22.5	14.2	S	3021
3026	2	♀	5.4	3.9	3.1	8.8			T-7	3024
		♀	4.7	4.0	3.0	8.5	22.8		T-7	3025

[1] Most measurements taken within 2 hours after birth, all taken within a 12-hour period.

ten days shorter than the gestation period for ten white-tailed deer in Michigan (Haugen and Davenport, 1950) and is roughly six days shorter than the previously published record for 21 whitetails (Taylor, 1956). In some cases the gestation period was known to within a matter of minutes as the actual process of birth was observed (Haugen and Speake, 1957).

In three out of four cases, the does dropped single fawns the first time bred. The second time they were bred, three out of four does dropped twins.

On an average the fawns from these Alabama deer were slightly smaller than whitetails in Michigan (Tables 4 and 5). Female fawns produced by the Alabama deer weighed 5.6 lbs.; the males averaged 6.2 lbs.

TABLE 5.—*Comparative average measurements of fawns in Alabama and in Michigan (linear measurements in inches)*

		AVERAGE WEIGHT, LBS.	TAIL LENGTH	EAR LENGTH	HINDFOOT LENGTH	TOTAL LENGTH	SHOULDER HEIGHT
Alabama	♀	5.6	4.0	3.0	8.7	23.8	14.8
	♂	6.2	4.2	3.1	9.1	24.4	15.0
No. based on:		18	16	16	15	13	12
Michigan[1]	♀	5.7	4.0	3.0	9.6	24.2	
	♂	7.4	4.6	3.4	10.3	26.1	

[1] After Haugen and Davenport, 1950. Weights based on 29, other measurements on 27 fawns.

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SUMMARY

The mating behavior of captive white-tailed deer in Alabama has been recorded. Does permitted copulation only on the one day they were in heat. Copulation was evidenced by a final lunge by the buck, which usually knocked the doe to her front knees or rammed her entirely off her front feet.

Half of the fawns were dropped between August 3 and 8, with the average gestation period for 12 pregnancies being 193.8 days. Average weights of whitetail fawns were 5.6 lbs. for females and 6.2 lbs. for males. Fawns from Alabama were slightly smaller than previously reported fawns from Michigan.

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MICROSCOPIC STRUCTURE AND VARIATION IN THE CUTANEOUS GLANDS OF THE DEER, *ODOCOILEUS VIRGINIANUS*

By W. B. Quay

The microscopic structure and the variations correlated with age and sex in three specialized glandular areas of the skin form the subject of this report. The three areas are commonly referred to as the tarsal gland, metatarsal gland and interdigital glands. The locations and gross aspects of these areas are diagrammed for this species in Plate I. The presence and structure of the various cutaneous glandular areas in artiodactyls varies greatly and is of interest not only from the standpoint of comparative histology and histochemistry but

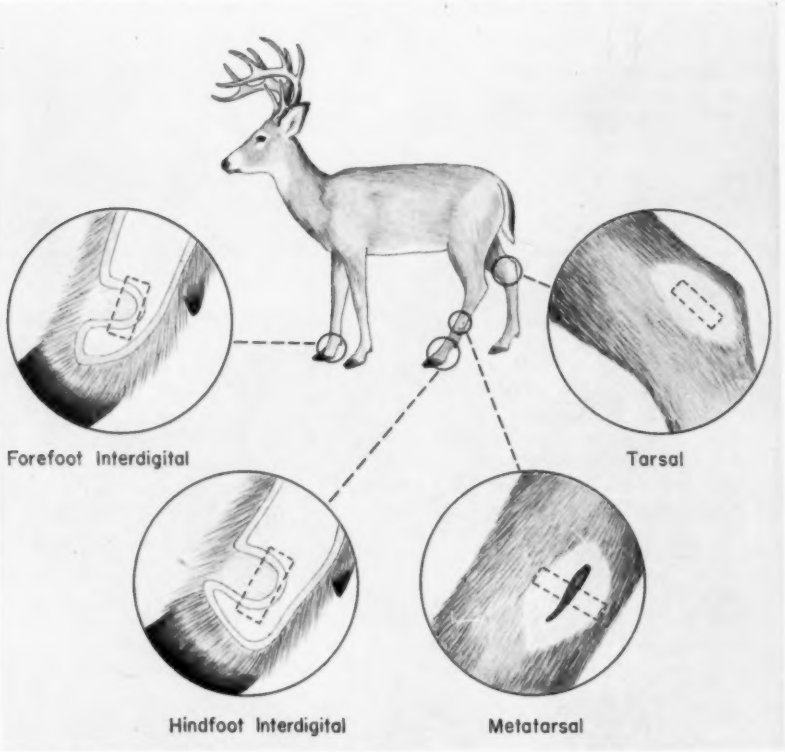

PLATE I

The locations of the glandular areas discussed in this report are diagrammed here; from left to right: forefoot interdigital gland, hind foot interdigital gland, metatarsal gland, and tarsal gland. The areas usually selected for microscopic examination are outlined with broken lines. However, in at least a few of the specimens several different portions of each area were sectioned and examined.

also in relation to behavior and phylogeny. The last major review of the skin glands in this and other mammalian groups is the monograph by Schaffer (1940). Although this subject has received attention for many years, there is still a great amount of confusion and there are many genera and species that have never been microscopically examined. The complexity of this subject stems largely from the following circumstances: (1) It is known that marked interspecific and intergeneric variation exists in the cutaneous glands of some artiodactyls, but in most cases this is incompletely documented; (2) significant changes with age, sex and season are likely in at least some of the glandular areas, but these have rarely been described; (3) the greatest amount of descriptive information and theorizing has been based upon macroscopic structure, which is sometimes a poor or erroneous indicator of glandular activity. The preorbital pocket and forefoot interdigital glands of the caribou are examples of the last of these situations (Quay, 1955).

The special glandular areas of the skin in deer of the genus *Odocoileus* have been briefly described for some species, mainly from macroscopic examinations, by Caton (1877), Pocock (1910, 1923), Cowan (1936) and Linsdale and Tomich (1953). The first three of these authors indicated that interspecific differences and significant taxonomic characteristics may be discerned in the glandular areas. And all of the authors suggested possible functions for them. Published anatomical findings and functional correlations will be considered subsequently in relation to the results present here.

I am grateful to Ralph S. Palmer and the New York State Department of Conservation for the skin samples used in this study, and for the accompanying data. I wish to thank also Emily Reid for Plate I and Victor Duran for the photomicrographs.

MATERIALS AND METHODS

The specimens used in this study consist of animals of both sexes and all ages from 3–4 months to 21½ years. Unfortunately, since nearly all of the animals were obtained in November or December, a study of seasonal variations in the glands is not possible at this time. The biological and historical data available for the specimens are listed in Table 1.

The skin samples containing the glandular areas were fixed in Bouin's fluid and stored in 70–80 per cent ethanol for varying periods of time. Paraffin sections 5 to 10 microns in thickness were stained either with Ehrlich's acid hematoxylin and eosin Y (Bensley and Bensley, 1938) or with a modified Taenzer-Unna acid orcein method for elastic fibers, with an Azure II counterstain (Lillie, 1948), or with a combination of these techniques.

RESULTS

Tarsal gland.—As noted by Cowan (1936), the tarsal gland is marked by a tuft of long coarse hairs on the median side of the tarsal joint (see Plate I) and consists of a thickened area of skin containing enlarged sebaceous and sudori-

TABLE 1.—*List of specimens and their data*

SPECIMEN NO. AND SEX	AGE AND/OR WEIGHT	DATE OF DEATH	LOCALITY	ANTLERS	REPRODUCTIVE STATUS AND GENERAL REMARKS
1 ♂	139 lb.	mid Nov.	——	4 points	
2 ♂	140 lb.	mid Nov.	——	4 points	
3 ♂	152 lb.	mid Nov.	——	8 points	
4 ♂	140 lb.	mid Nov.	——	8 points	
5 ♀	•3–4 mo.	late Nov. '52	Albany Co.		
6 ♀	150 lb.	Nov. 8, '48	St. Lawrence Co.	antlered	
7 ♂	abt. 1½ yr.	Dec. 2, '52			
8 ♀	•abt. 1½ yr.	Nov. 6, '52	Tompkins Co.		
9 ♀	abt. 5½ yr.	Dec. 17	——	——	Castrated and penned animal
10 ♀	21½ yr.	early Dec.,'53	Vermont	——	Oldest known ♀; born June 8, 1932; never bred; always penned; death due to broken neck, Dec. 1953
11 ♀	4½ yr.	Dec. 11, '53	——	——	Bred at least twice; penned
12 ♀	3½ yr.	Dec. 11, '53	——	——	Never bred; penned
13 ♀	•7½ yr. 150 lb.	Nov. 22, '51	Albany Co.	antlered	Pregnant 1950–51; lactating Nov. 22; adrenals, uterus and ovaries normal, latter with regressing corpora lutea; antlers and reproductive system described by Wislocki (1954)
14 ♀	•2½ yr. 129 lb.	Nov. '51	Chautauqua Co.	antlered	Milk in udder, uterus small, ovaries atrophic and contained a regressing corpus luteum but no secondary follicles; pituitary normal grossly; antlers and reproductive system described by Wislocki (1954)
15 ♂	11–12 mo.	June 5, '51	Albany Co.	each 3 in.	In fresh summer pelage

• Age determined by C. W. Severinghaus on basis of tooth development or wear (Severinghaus, 1949).

ferous or sweat glands. This author also stated that the sebaceous glands present the greatest enlargement and comprise the bulk of the secreting ele-

PLATE II

LEFT: Vertical section through the middle of the tarsal gland area of specimen No. 9.
RIGHT: Vertical section through the middle of the most glandular portion of the metatarsal gland of specimen No. 12.

Both were stained according to a combined hematoxylin-eosin and orcein procedure. A—arteries; AG—apocrine sudoriferous gland tubules; AM—arrector pili smooth muscles bundles; E—epidermis; HF—hair follicles; SG—sebaceous glands.

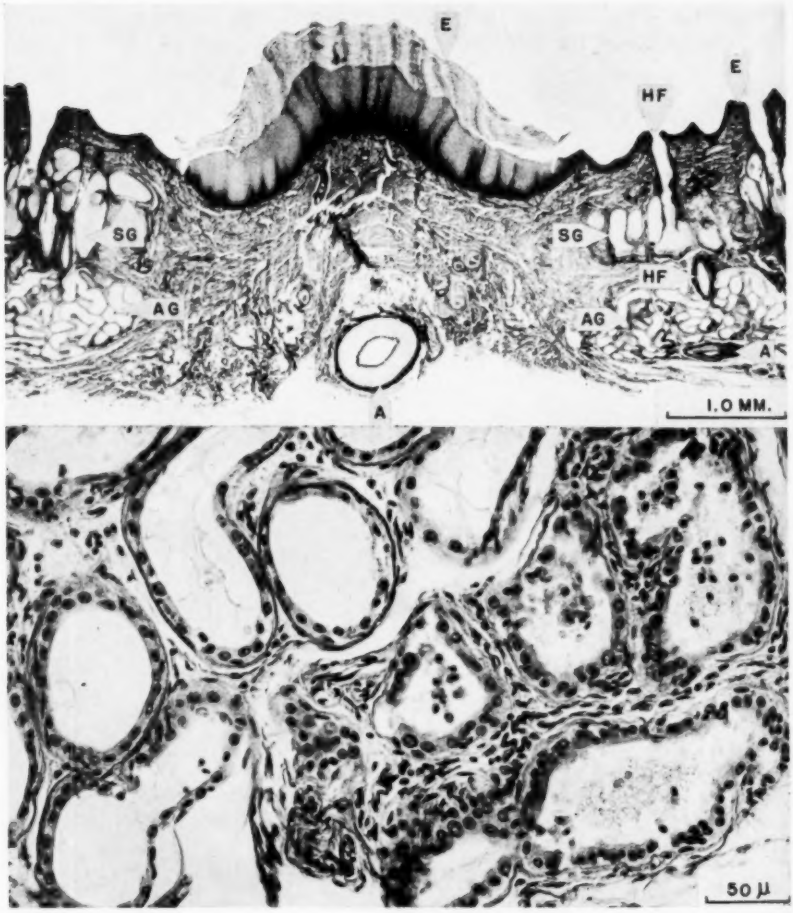

PLATE III

TOP: Cross section of the middle of the metatarsal gland of specimen No. 9, showing the keratinized patch of epidermis overlying dense connective tissue and central artery. The sharp demarcation of the keratinized patch and the glandular areas is shown. This section, 10 microns in thickness, was stained according to a combined hematoxylin-eosin and Azure-orcein technique. Abbreviations as in Plate II.

BOTTOM: Small area of apocrine tubules in the metatarsal gland of the oldest female (specimen No. 10), showing relatively active and normal secretory tubules at the upper left and degenerating tubules at the lower right. In the latter, note the pyknotic and giant cells in the walls of the tubules as well as the pyknotic cells being sloughed into the lumen. Fibrosis in the stroma is also seen in the lobule containing degenerating tubules. This section was stained with hematoxylin and eosin.

ments. This seems to be generally true in my material as well.

The histology and general structure of the tarsal gland area in the Virginia deer is similar to that described previously in the caribou (Quay, 1955). The epidermis is not especially thickened, and has a depth of 17 to 52 microns or 5 to 7 nucleated cells. The dermis, composed of two layers, presents a superficial layer containing hair follicles, sebaceous glands, arrector pili muscles and connective tissue stroma containing many elastic fibers; and a deeper layer containing apocrine sweat glands and delicate, frequently adipose, connective tissue. Bounding the deeper layer internally is a layer of dense fibro-elastic connective tissue (Plate II, left).

Although the basic plan and structure of the tarsal gland in the Virginia deer are similar to those of the caribou, there are several significant, primarily quantitative, differences. (1) In none of the adult deer does the layer of apocrine sweat glands attain the average thickness (1.45 mm.) shown in the adult female caribou, and in none of the deer is this layer as thin (0.35 mm.) as it is in the male caribou. (2) In many of the deer, fat or adipose tissue forms from 10 to 50 per cent of the contents of the apocrine layer. Adipose tissue was not found in the apocrine layer of the caribou. (3) The superficial layer of the dermis is thicker and its component parts, particularly the arrector pili muscles and hair follicles, are larger in all of the adult deer (Table 2) than in the caribou (1.55 mm. in ♀, 1.07 mm. in ♂). The arrector pili muscles reach a size of 3.4 × 0.22 mm. in deer No. 13 and even in the 3–4-month-old deer (No. 5) the muscles are about 1½ times the size of those in the adult caribou (1.7 × 0.17 mm.). On the other hand, the sebaceous glands in the superficial layer of the dermis are not noticeably larger nor more numerous in the deer as compared with the caribou. (4) The tarsal glands of the caribou show a much greater development in the female than in the male, and this is most apparent in the apocrine glandular portion (Quay, 1955). The Virginia deer shows only a slight indication of greater tarsal glandular area development in the female and this is somewhat more clearly indicated in the superficial layer of the dermis with its arrector pili smooth muscles than elsewhere in the area.

Measurements of significant structures and areas in the tarsal glands (Table 2) show the great range of individual variation. It appears that the tarsal gland is in a functional state in the youngest animals and increases in area during early life.

Metatarsal gland.—The metatarsal gland is an area of highly modified skin on the posterolateral side of the metatarsus, slightly below the halfway point (Plate I). The gross aspects and intergeneric variations of the area have been studied particularly by Caton (1877), Zeitzschmann (1903), Pocock (1923) and Cowan (1936). There appear to be well-defined species differences and quantitative racial differences in the superficial morphology of the area in the genus *Odocoileus*. However, adequate sets of measurements and thorough analyses of possible age, seasonal, sexual and racial differences have yet to be presented.

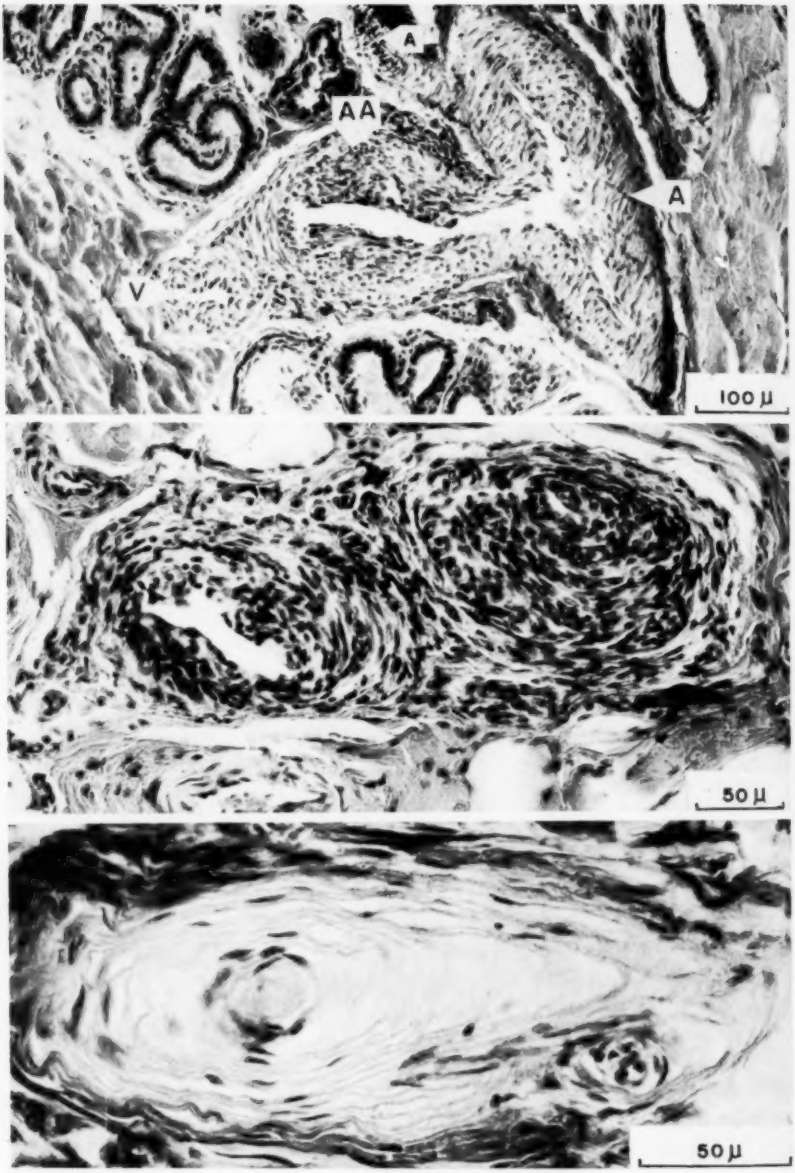

PLATE IV

TOP: A large arteriovenous anastomosis from the metatarsal gland of specimen No. 1. Running obliquely through the right of the section and below the apocrine glandular layer is is major artery (A) which gives rise to one arteriole (A) in the field as well as a large arterio-

PLATE V

Small area in a vertical section through the fundus of the hind foot interdigital gland of specimen No. 9, stained by a combined hematoxylin-eosin and orcein procedure. Note the lack of apocrine glands and the large size of the sebaceous glands, hair follicle (gland duct) and the arrector muscles. AM—arrector pili smooth muscle bundle; E—epidermis; HF—hair follicle; HS—hair shaft; SG—sebaceous glands.

venous anastomosis (AA) which leads into a venule (V).

MIDDLE: A thick-walled arteriovenous anastomosis from the metatarsal gland of specimen No. 1. Two portions of the same coiled anastomosis are shown here in cross section.

BOTTOM: A sensory corpuscle from the central area of the metatarsal gland of specimen No. 15.

All were stained with hematoxylin and eosin.

In our specimens, the metatarsal gland area consists grossly of an elliptical patch of heavily keratinized and pigmented, hairless skin surrounded by a band of skin supporting stiff, whitish hairs and enlarged cutaneous glands. The keratinized patch runs parallel to the axis of the metatarsus and its dimensions range from 2½ × 20 mm. in a 3–4-month-old fawn to 5½ × 33 mm. in a 3½-year-old doe (Table 3) in fixed pieces of skin. It is of reduced size (2 × 27 mm.) in the oldest doe (No. 10, 21½ years). Accurate measurements of the band of white-haired and glandular skin are not now available.

The keratinized patch of epidermis, representing the center of the modified area of skin, demonstrates the strata typical generally of areas of thick, keratinized mammalian epidermis. And the stratum granulosum is usually several cells thick. Above this layer, the epidermal cells become eosinophilic and have pyknotic nuclei, before becoming featureless, cornified scales. The total thickness of the epidermis here is variable (Table 3), due in part to variable degrees of post-mortem desiccation. One of the most striking characteristics of this metatarsal patch of thickened epidermis is the presence of numerous, high, connective tissue papillae, which penetrate the epidermis from below and reach to within a few microns of the stratum granulosum. Within the papillae are capillary loops and delicate strands of connective tissue. Specialized or encapsulated sensory endings are not discernible in the papillae in the preparations stained with hematoxylin and eosin. Nevertheless, such endings may yet be disclosed here with the aid of techniques better suited for this purpose. Beneath the ellipse of highly keratinized epidermis is dermal connective tissue, without any glandular tissue or hair follicles. The more superficial two-thirds to one-half of this connective tissue is dense and contains, primarily, heavy collagenous fibers with scattered, small and few elastic fibers. The deeper portion of the dermis under the keratinized patch contains areas of more delicate connective tissue as well as scattered areas of adipose and dense collagenous connective tissue. The deep dermal areas of delicate connective tissue contain either numerous small capillaries, arterioles and venules, or they contain arteriovenous anastomoses surrounded by numerous small vessels. In its basal portion, the dermis under the keratinized patch always contains one or two arteries, the largest in the metatarsal glandular area. These *central arteries* run parallel to and directly under the keratinized patch and range from about 0.5 to 0.8 mm. in outside diameter in the fixed and stained preparations. Concentrically encapsulated structures, probably representing specialized sensory endings for either pressure or temperature, are occasionally seen in the deeper dermis above and not far from the central artery or arteries (Plate IV). One such sensory corpuscle averages about 80 μ in outside diameter and is composed of about 20 concentric layers of delicate connective tissue fibers and fibrocytes.

The arteriovenous anastomoses in the metatarsal dermis appear to be numerous and most prevalent in the area beneath the central keratinized patch. But they occur frequently also in the dermal connective tissue of the glandular

TABLE 2.—*Measurements of significant structures or areas in the center of the tarsal glandular area. Measurements under 5 mm. were made*

TABLE 2.—*Measurements of significant structures or areas in the center of the tarsal glandular area. Measurements under 5 mm. were made with the aid of an ocular micrometer. No tarsal gland tissue samples are available from specimen No. 10, and those from Nos. 13 and 14 (*) are poorly preserved. Increased epidermal height in the younger animals and an only slight sexual difference in dermal thickness are shown*

SEX:	MALES						FEMALES							
AGE:	11–12 MOS. →				ADULTS →		3–4 MOS. →			ADULTS →		ANTLERED		
Specimen No.	15	7	1	2	3	4	5	8	12	11	9	6	13*	14*
Epidermal thickness:														
number of nucleated cells	7	5	6	6	5	6	6	7	5	6	6	5	6	5
microns	52	17	22	24	18	21	32	36	34	33	23	22	22	18
Thickness of superficial layer of dermis (mm.)	2.07	1.77	1.72	2.15	2.84	2.20	1.51	2.33	2.50	2.38	2.41	2.16	2.93	2.50
Thickness of apocrine glandular layer of dermis (mm.)	0.91	0.43	0.73	1.12	1.03	1.17	0.52	1.03	0.86	1.23	1.34	0.82	1.33	0.78
Total dermal thickness (mm.)	2.98	2.20	2.45	3.27	3.87	3.37	2.03	3.36	3.36	3.61	3.75	2.98	4.26	3.28
Average height of aprocrine secretory cells (microns)	14	9	16	10	14	8	12	11	11	6	16	8		
Dimensions of tarsal gland area in excised and fixed skin (mm.)	—	—	—	—	—	50× 60	35× 40	—	—	—	45× 65	45× 60		

* Poor preservation.

TABLE 3.—*Measurements of significant structures or portions of the metatarsal gland. All measurements except those given as dimensions of the keratinized patch were made with the aid of an ocular micrometer. Significant age or sexual differences are not apparent*

SEX:	MALES						FEMALES					
AGE:	11–12 MOS. →			ADULTS →			3–4 MOS. →			ADULTS →		ANTLERED
Specimen No.	15	7	1	2	3	4	5	8	12	11	9	13*
Epidermal thickness in keratinized patch (microns)	350	—	420	670	600	430	470	530	430	600	600	430*
Dimensions of keratinized patch (mm.) in excised and fixed skin	3× 16	4× 23	—	4× 20	—	—	2½× 20	4× 15	5½× 33	3× 25	3× 22	5× 29
Thickness of sebaceous glandular layer of dermis (mm.)	1.20	—	1.12	1.20	1.07	1.20	1.00	1.20	1.30	1.40	1.35	1.00
Thickness of apocrine glandular layer of dermis (mm.)	0.95	—	1.16	0.90	1.20	1.30	0.60	0.95	1.00	1.10	1.00	*

* Poor preservation.

zone adjacent to the central patch. In the glandular zone the anastomoses occur in the connective tissue between the apocrine sweat (deep) and sebaceous (superficial) glandular zones and in the septa between individual apocrine tubules. The anastomoses vary from 50 to 130 microns in outside diameter and are short vessels connecting normal arteries of about the same size (40 to 130 microns) with small veins, thus bypassing the arteriolar and capillary circulation. The structure of the vessel wall in the anastomoses is much different from that of the associated artery and vein. The thick medial zone of circular smooth muscle in the artery becomes reduced. And it is progressively replaced on its internal side by longitudinally and spirally arranged masses of modified smooth muscle or epithelioid cells. In its end portion the anastomotic segment has an extremely thick wall of these cells, few elastic fibers, and a lumen only 10 to 30 microns in diameter (Plate IV). Arteriovenous anastomoses are characteristic of various peripheral areas in a wide variety of mammals, such as in the dog's tongue, rabbit's ear, calves' ears, forehead and cheek. There are apparently marked generic and ordinal differences in their distribution in the body. The most widely accepted belief is that these structures regulate blood circulation and pressure in various parts of the body. It has been shown that as a result of these activities in the rabbit's ear, the anastomoses take part in temperature regulation both of the body generally by facilitating heat loss through increased peripheral circulation and of the local area by temperature maintenance against local cooling (see especially Grant and Bland, 1932).

The glandular band of the metatarsal glandular area borders on and is sharply differentiated from the central keratinized zone (Plate III). In contrast with the adjacent unspecialized and haired skin, the glandular band has: (1) A thicker dermis; (2) fewer but larger hairs, which are whitish in color and more vertical in position; (3) reduced arrector pili smooth muscle bundles; (4) enlarged sebaceous glands; and (5) enlarged apocrine sweat glands. The dermal zonation with hair follicles and sebaceous glands above the apocrine glandular zone is basically the same in the metatarsal area as it is in the tarsal glandular area, but the sebaceous gland zone is always thicker in the tarsal glandular area (Tables 2 and 3) and differs markedly in its content of relatively huge arrector pili muscles. In the metatarsal glandular area, arrector pili muscle bundles are difficult to find and the maximum diameter ranges from 10 to 40 microns. This is 5 to 20 per cent of the maximum diameter of the bundles in the tarsal patch. In the most peripheral part of the metatarsal glandular band, the apocrine tubules frequently appear atrophic, even in young adults. There is great variation in the cytologically apparent activity both in adjacent apocrine glands and in apocrine glands in different individuals. This is evident in secretory tubule diameters, amounts of luminal secretion, height of the cytoplasm in secretory cells and atrophic changes in the tubules. There is no indication of significant sexual dimorphism in the microscopic anatomy of the metatarsal glands. Secretory activity is evident in the metatarsal apocrine and sebaceous glands of the 3–4-month-old fawn as well as in the 21½-year-

old doe. However, in the latter animals the glands are larger and almost half of the apocrine glands show regional or general atrophic changes (pyknosis and sloughing of cells into the lumen) as well as cytological abnormalities (binucleate and giant nucleated cells) (Plate III). In the old doe, the degenerating apocrine glands seem to be scattered at random among apocrine glands of nearly normal appearance throughout the metatarsal glandular area. In the younger animals (Nos. 5 and 15) only the apocrine glands that are most peripheral in the metatarsal area show degenerative changes.

Interdigital glands.—The interdigital glands are glandular areas in the dorsal interdigital skin (Plate I). In this species the interdigital glands have the form of pockets between the primary digits of both the fore and hind feet.

Tissue samples of the interdigital glandular areas in the Virginia deer are available from only three of the specimens (forefoot: Nos. 10, 11, 14; hind foot: Nos. 9, 10, 11). Therefore, definitive considerations of age and sexual variations must be postponed. Although in nearly every case an extensive area of the fundus of each interdigital gland was sectioned, some uncertainty remains regarding the occurrence and distribution of apocrine sweat glands in the interdigital pockets. In most specimens apocrine glands are either lacking or very few in number in both the forefoot and hind foot interdigital glands. In specimen No. 11, however, a distinct layer of apocrine glands forms a continuous zone about 0.5 mm. thick under the sebaceous glands. In all specimens, the interdigital pockets are characterized primarily by greatly enlarged sebaceous glands, forming a superficial zone in the dermis 1.1 to 1.4 mm. in thickness. These glands empty their secretions into dilated hair follicles, each of which contains shafts of hair 40 to 70 microns in diameter. The follicles appear to owe their large size to their activity as gland ducts and their content of masses of sebaceous secretion compounded with layers of cornified cells released from the stratified and keratinized epithelium lining the ducts. The epithelium of the enlarged follicles is thickened and is continuous with the epidermis, which is thicker than in adjacent areas of digital skin. The basal portion of the epidermis including the stratum granulosum varies in thickness from 30 to 100 microns.

The dermis of the interdigital pockets is characterized by abundant elastic fibers and enlarged arrector pili muscles, as well as by enlarged and specialized sebaceous glands. The elastic fibers are largest and most numerous in the more superficial half of the dermis and they form a delicate elastic lamina around each enlarged follicle or sebaceous gland duct and lie in intimate contact with the basal cells of the epithelium. The arrector muscles extend from the basal part of each follicle to the epidermis, bowing outwardly over the intervening sebaceous glands. The maximum belly diameter of these muscles varies from 70 to 210 microns.

There is some evidence in the limited material at hand that the interdigital sebaceous glands enlarge progressively with age, and that this is demonstrated most strongly in the size of the lumen of the gland duct or follicle. Age changes

in the apocrine glands are also likely. The interdigital apocrine glands of specimen No. 11 show little evidence of degeneration and no intracellular pigment. In contrast, these glands in the oldest doe (No. 10) are nearly all atrophic and many of the secretory cells contain pigment granules of a yellow to golden-brown color. This is the only instance in which pigment was found in the apocrine glands of *Odocoileus*. In the caribou, apocrine pigment-containing cells were found only in the interdigital glands and here the glands are much larger than those in *Odocoileus* and are not atrophic (Quay, 1955).

DISCUSSION

The tarsal gland in at least some members of the genus *Odocoileus* appears to function by erection of its coarse and differently colored hairs and by glandular secretion especially during times of rut in males, irritation, warning and fright (see especially Caton, 1877; Nichol, 1938; Linsdale and Tomich, 1953). In *O. virginianus*, the microscopic structure as well as the size and white basal coloration of the tarsal tuft suggest that glandular secretion is less important here than erection of the tuft of hair as a method of silent communication between numbers of the species. Sexual distinctions are only barely apparent as yet in the tarsal glands of this species and may possibly be shown in the future to be more marked at other seasons of the year. The tarsal patch and area, from the results presented here, appear to be designed primarily for visual communication in Virginia deer of all ages, and the scent-producing modality may not be as significant as it is in other species of this and other genera.

The metatarsal "gland" of the Virginia deer contains not only an area of enlarged and probably scent-producing glands, but also a nonglandular and heavy keratinized area that may have sensory functions as well as housing a set of large arteriovenous anastomoses that may help to regulate both the blood supply of the distal parts of the hind legs and body temperature. When the deer reclines, the metatarsal gland of one side is brought into contact with the ground, probably leaving a scent as well as making a closer juxtaposition of sensory endings in the metatarsal patch with the substrate. The apocrine sweat or sudoriferous glands are the most prominent elements in the glandular zone bordering the keratinized patch, but the sebaceous glands, hairs and hair follicles are also enlarged. In contrast, the arrector muscles of the hairs are not well developed, and although the hair in the area is lighter in color and longer, its capacity for erection by muscular means must be poor in comparison to that of the tarsal patch.

The interdigital glands in this species are most notable for the great enlargement of the sebaceous glands and to a lesser extent for the enlarged arrector pili muscles, which must serve here primarily to force glandular secretion from the ducts and hair follicles into which it passes. Considering the breadth of the variation in the development of the interdigital glands in artiodactyls and

the location of the glands, the most likely and significant function appears to be associated with the leaving of scent.

The gross and microscopic structure of these three glandular areas in *O. virginianus* differs greatly not only from that in the caribou (*Rangifer*), but also from that in the western species of the genus *Odocoileus*. However, the published information on the microanatomy in the latter species is meager (see Cowan, 1936; Linsdale and Tomich, 1953). The three areas appear also to be functional in animals of all ages in *O. virginianus* and little if any sexual dimorphism is discernible in the material available at this time.

SUMMARY

The material used in this study consists of skin samples from 15 deer (*Odocoileus virginianus*) taken in nearly all cases in November or December in the State of New York and representing various ages from 3–4 months to 21½ years, both sexes and three antlered does.

Microscopic study of stained paraffin sections of three specialized cutaneous glandular areas demonstrates the following features: (1) The tarsal glandular area in this species is most notable for its content of greatly enlarged arrector pili smooth muscle bundles and the associated lightly colored and enlarged hairs, which may serve in a specialized manner for visual communication by erection. The glandular elements, both sebaceous and apocrine sudoriferous, while somewhat enlarged in the tarsal "gland" area, do not approach the glandular development seen in the tarsal "gland" area of certain other species and exhibit slight if any sexual dimorphism. (2) The metatarsal "gland" consists of two histologically different and perhaps functionally different areas, a central glandless area supporting a thick and keratinized epidermal patch, and a bordering highly glandular area, containing enlarged sebaceous and apocrine sudoriferous units. The keratinized patch is high papillated and overlies numerous arteriovenous anastomoses and some specialized sensory endings, which may be associated with control of blood flow in the distal parts of the hind legs and in temperature regulation. The metatarsal glandular elements may serve to leave scent in areas where the animal reclines. (3) The interdigital glands in this species contain primarily greatly enlarged sebaceous glands which empty into dilated hair follicles and may be aided by unusually large arrector pili muscles. The scarcity of interdigital apocrine sudoriferous glands in the interdigital glandular pockets may be a distinctive feature of this species. The interdigital glands appear to be designed primarily for leaving a scented trail for other members of the species.

The three specialized glandular areas appear to be active in animals of all ages and little if any significant sexual difference is seen in our material. Degenerative changes occur first in the apocrine glandular elements and are most marked in the oldest (21½ years) doe. No significant correlations with the antlered condition present in three of the does were found.

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SMALL MAMMAL STUDY IN WEST-CENTRAL OREGON

BY JAY S. GASHWILER

The lumbering and wood products industry is the most important in the Pacific Northwest. As more old-growth timber is harvested, farsighted people are becoming increasingly concerned about managing the resource on a sustained yield basis. A major problem confronting foresters is to get prompt and full restocking of clearcut areas. Small seed-eating mammals, primarily deer mice, are one of the factors responsible for poor stands of seedlings (Moore, 1940). Considerable research has been done on small mammals, but additional basic information is needed on their relationship to the staggered-setting system of clearcutting widely practiced in western Oregon and Washington. In an attempt to secure some of this information, a project was started on the H. J. Andrews Experimental Forest in April, 1954. This progress report includes data on small mammals secured until the end of November, 1956.

The major objectives of the study were (1) to measure the small mammal populations in virgin, recently logged, and recently burned forest habitats; (2) to gather as much information as possible on the mechanics of small mammal population fluctuations after logging and burning.

This study was made in cooperation with the Pacific Northwest Forest and Range Experiment Station, U.S. Forest Service. I am especially grateful to R. H.

Ruth, R. R. Silen and H. J. Gratkowski, all of the Station; and to Leo A. Isaac and R. C. Koenig, formerly of the Station. Their kind suggestions, consideration and assistance were very helpful during the study. I would also like to acknowledge the fine cooperation of Dr. Albert N. Steward, Oregon State College Herbarium, and Mike M. Savelich, Eugene, who logged the 5B unit.

LOCATION AND TOPOGRAPHY

The H. J. Andrews Experimental Forest is typical of timber-harvesting areas of the region. It is located in central Oregon on the west slope of the Cascade Mountains in Linn and Lane counties. The forest includes the entire watershed of Lookout Creek, a tributary of Blue River. Lookout Creek flows in a westerly direction, and the forest is composed primarily of northerly and southerly exposures. Elevation varies from about 1400 feet at the lowest point to 5250 feet on top of Lookout Mountain.

STUDY UNITS

A 48-acre area (5B) scheduled for clearcutting was selected for study. It had a southerly exposure with an average slope of approximately 18 per cent and an elevation ranging from about 2900 to 3500 feet. It was typical of the general forest terrain, being bench-like with relatively steep intervals. The unit was in virgin forest at the start of the study, and surrounding timber offered an opportunity for movement lines and an isolated virgin timber control grid. Logging started in June, 1955, and ended the following October when the slash was burned. The experimental grid was established in the 5B cutting at the 3050-foot level.

Movement lines were located laterally from each side of the experimental grid. They were in essentially the same timber type with approximately the same slope and elevation.

The control grid was located in old-growth timber about 1900 feet from the nearest logging operation and was essentially free from man-caused disturbance. Its elevation was near the 3450-foot level. The slope was toward the south but was less abrupt than the experimental grid.

VEGETATION

Virgin timber.—The timber on the study area was primarily old-growth Douglas-fir (*Pseudotsuga menziesii*). Some of the trees were over 400 years old and were starting to break up—a few had their tops broken, others were blown over, and still others were dead and starting to decay. Wherever there was an opening in the stand, shade-tolerant western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) reproduction was present. The volume of sound timber logged on the 5B unit was:

Species	*Board feet*	*Per cent*
Douglas-fir	2,362,580	86.6
Western hemlock and others	330,330	12.1
Western red cedar	34,730	1.3
Total	2,727,640	100.0

The composition of species in the Douglas-fir belt varies considerably, but the percentages for the 5B unit appear to be about average for the type.

Ground cover.—Ground-cover data were obtained from an area of 600 × 650 feet superimposed on the small-mammal grids. Four randomized lines were run across each unit with permanent milacre plots taken at 50-foot intervals. The sample for each unit consisted of 56 plots. Logging and burning destroyed the markers but they were relocated as close as possible to the original sites. Ocular estimates of the percentage of shade cast by each species on the

TABLE 1.—*Ground cover (per cent of total) on the virgin timber control area (Area A) and the experimental area (Area B) prior to cutting (1954) and at end of first growing season after logging and burning (1956)*

SPECIES COMPOSITION	AREA A		AREA B	
	1954	1956	1954	1956
Herbaceous plants:				
Gold-thread, *Coptis laciniata*	19	19	21	3
Twin-flower, *Linnaea borealis*	20	18	12	1
Sword fern, *Polystichum munitum*	9	9	6	3
Rattlesnake plantain, *Goodyera decipiens*	9	9	1	
Violet, *Viola* sp.	2	3	6	2
Starflower, *Trientalis europaea*	1	1	–	8
Cool-wort, *Tiarella unifoliata*	1	1	4	
Lady fern, *Athyrium felix-femina*	–	–	1	
Oats, *Avena sativa*	–	–	–	4
Whipplea, *Whipplea modesta*	1	1	–	4
Inside-out flower, *Vancouveria hexandra*	–	1		
Meadow-rue, *Thalictrum occidentale*	–	1		
Groundsel, *Senecio vulgaris*	–	–	–	2
Brome-grass, *Bromus* sp.	–	–	–	1
Miscellaneous	3	3	3	1
Total	65	66	54	29
Brush plants:				
Mountain Oregon grape, *Berberis nervosa*	9	8	15	3
Salal, *Gaultheria shallon*	7	7		
Vine maple, *Acer circinatum*	6	6	13	13
Wild blackberry, *Rubus macropetalus*	4	4	7	45
Huckleberry, *Vaccinium* sp.	4	4		
Rhododendron, *Rhododendron macrophyllum*	2	2	3	
Snow bramble, *Rubus nivalis*	1	1	5	1
Prince's pine, *Chimaphila umbellata*	1	1	1	1
Common dogwood, *Cornus nuttallii*	–	–	1	
Western hazel, *Corylus rostrata*	–	–	–	3
Wood rose, *Rosa gymnocarpa*	–	–	–	1
Wild cherry, *Prunus emarginata*	–	–	–	1
Cinnamon bush, *Ceanothus velutinus*	–	–	–	1
Miscellaneous	1	1	1	1
Total	35	34	46	69
Miscellaneous and conifers	0	0	1	2
Average density of total cover	17	19	22	2

available seed bed were made. An estimate was also made of the density of all ground cover on each plot. Only plant species comprising one per cent or more of the ground cover were included in the compilations.

Ground cover was measured on the control grid and on the experimental area during August and early September, 1954, when both were still in their virgin state. Another survey was

made during August, 1956, after the logged and burned experimental area had gone through one growing season following the fire.

There was only a slight increase in the density of the ground cover on the control area during the two-year period (Table 1). The species comprising the sample and their percentage are essentially the same. That variation which does occur is probably the result of sampling error rather than a change in cover.

The results of the ground-cover survey on the experimental area are also given in Table 1. Ground-cover density dropped from 22 to 2 per cent, and the composition changed from a predominately herbaceous to a woody or brushy type the first growing season after burning. It is of interest to note that very few wind-borne seeded species were present on the area. This was probably the result of late burning which came after the main period of seed dispersal and destroyed most of the seeds which previously had drifted onto the area. The great increase in the percentage of wild blackberies is worth note; under virgin forest conditions they are suppressed. Oats which were recorded came from the live-trap bait. Very few seeds were produced by plants on the experimental area the first growing season after burning. Their value to the small mammals for food must have been so slight as to be almost nil. However, the plants did produce some vegetative material which could have been used for food.

The post-burning ground-cover data for the experimental unit do not correspond with that given by Isaac (1943). He found a plant density of 35.4 per cent the first growing season after the burn, and a preponderance of herbaceous species. The bulk of his herbaceous vegetation was composed of wind-borne seeded species which were nearly absent in the present study. When these plants are deleted from Isaac's table, the two sets of data are more nearly comparable.

EFFECT OF BURNING ON THE SOIL

Many cull logs and much wood debris are left on cutting units after logging and, when dry, this constitutes a fire hazard. To reduce this hazard, foresters commonly burn these areas under controlled conditions. Burning also leaves more mineral soil exposed and many foresters consider this to be a superior type of seedbed for Douglas-fir.

Slash burning is generally done in late fall or early spring. Foresters try to select periods when the soil is moist but when the debris is dry enough to burn readily. Moist soil helps to reduce the loss of humus and lowers the fire hazard in green timber.

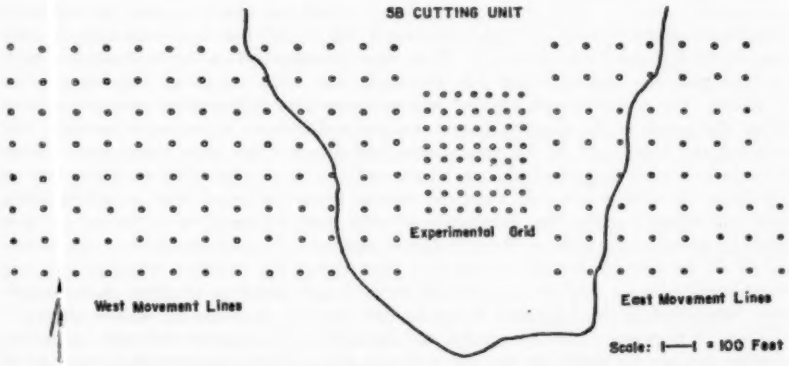

FIG. 1.—Map of lower 5B cutting showing trap sites on experimental grid and movement lines.

Fires were started at the top of the clearcut unit and were set progressively downward. The broadcast burning was started October 14, 1955, and progressed to within approximately 200 feet of the small mammal grid when operations stopped for the day; the remainder of the area was burned October 15.

The intensity of slash burning is dependent on many factors and is apt to vary within the same or different cuttings. The type of burn may affect the small mammal population. Therefore, it seemed desirable to measure the intensity of burn so different areas could be compared more accurately and the effect on the small mammal population could be better understood.

The intensity of the burn was measured on a 400 × 450 foot area superimposed on the experimental grid. Eight hundred randomized line point observations were made. Three classes of soil condition were recognized: (1) Unburned; most of the soil surface escaped burning; (2) Light burn; soil surface was mostly charred litter but some organic matter was not burned; (3) Severe burn; all organic matter burned and soil baked to highly colored state.

Results of this survey are:

Type of burn	*Per cent*
Unburned	46.1
Light burn	47.5
Severe burn	6.4
Total	100.0

The compilation compares favorably with the average for 10 Oregon clearcuts presented by Tarrant (1956). However, the percentage of severe burn was a little higher in the present study. Part of the landing fell within the sample and the large accumulation of cull logs caused severe burn; thus, the data may be biased on that account.

RESULTS AND DISCUSSION

Two small-mammal grids were established to investigate mouse populations in virgin, logged, and burned forest habitat. The control grid was placed in an isolated spot and the experimental grid was located within the 5B cutting unit. Each grid covered a 300 × 350 foot area and contained 56 trap sites spaced 50 feet apart (Fig. 1). The grids were made small so they could be run simultaneously, to avoid the influence of weather on the comparative catches. They were too small with traps too closely spaced for chipmunk population estimates; therefore, grids covering a 500 × 700 foot area containing 48 traps spaced 100 feet apart were also used. These were superimposed on the small-mammal grids and trapped one period during late fall each year when maximum populations were expected. The normal trapping period was six consecutive nights; there were a few times when the length of the trapping period was reduced because of excessive snowfall, cold weather and burning of the 5B area. Large-sized Sherman live traps baited with chicken scratch feed containing cracked corn, wheat and oats were used. Dry wool was kept in the traps for nesting material. Captured animals were ear-tagged with monel fingerling tags and released at the site. Population densities were estimated on an animal per acre basis by means of the ratio or "Lincoln Index" method. The final population estimate was based on the average for all but the first three days. The effective trapping area was considered to be the grid plus one-half the range length added to all sides. Range length was determined by the "Adjusted Range Length" method described by Stickel (1954).

Lines of traps were also set parallel and laterally to the experimental grid, across the cutting and into the timber on the east and west sides. These movement lines were set in an attempt to follow the movements of the small mammals between the cutting and the standing timber. Eight traps were spaced 100 feet apart in lines 100 feet apart. There

were eight lines east of the small-mammal grid and 13 to the west (Fig. 1). The traps were run for a period of three consecutive nights, with few exceptions, generally after the grids had been trapped.

DEER MOUSE (*Peromyscus maniculatus rubidus*)

Populations.—The *Peromyscus* population in an overmature Douglas-fir forest varied from 0.0 to 2.5 animals per acre depending on the time of year. During 1955, the population on the control grid had an early spring build-up, a summer recession and a late fall increase; this seems to be the normal population pattern for western Oregon. Because of the difference in elevation and slope, the control grid population for June, 1955, was more comparable with the population on the experimental grid in May.

The *Peromyscus* population was 1.5 to 1.9 animals per acre on the experimental grid during 1954. In May, 1955, the estimate increased to 2.5 animals per acre. Timber felling started on the experimental unit in June, 1955. By August, the grid was logged, and it was possible to resume trapping. It seemed unlikely that mice would persist on the area in the face of such great logging activity; however, the August trapping revealed a population of 2.0 deer mice per acre—just a little less than the last pre-logging population estimate in May. The *Peromyscus* population was 3.5 animals per acre in September and 3.4 per acre for the first part of October. Spencer (1955) found that slash constituted a favorable habitat for rodents.

The 48-acre area, including the experimental study plot, was burned October 14 and 15. Ten days after the fires were started, the grid was remarked and trapping was resumed. At that time, fires were still blazing on the area and smoke was sometimes quite dense. Ashes were loose and in places flowed over shoes six inches high. The *Peromyscus* did not seem to be unduly frightened by the fire—some were captured within two feet of a blaze. The October trapping indicated an estimated population of 4.0 deer mice per acre; this was slightly greater than the pre-burning estimate. By November, the population had increased to 6.2 per acre, or about double the pre-burning numbers and nearly three times the number on the same area the previous fall. At this post-burning population peak, the number of *Peromyscus* was about three times as great as the number on the control grid. The build-up on the experimental grid was partially due to the normal yearly population cycle; however, the freshly logged and burned area had some attraction for *Peromyscus*. It seemed strange that deer mice would be attracted to an area which was so devoid of vegetation but Stickel (1946) found that *Peromyscus* tend to move into depopulated range. Later it will be shown that the local deer mice were not seriously reduced in numbers by the fire, although many were driven from their homes, temporarily depopulating the area. Other investigators feel that burning does not entirely destroy the food resources of an area and enough remains to feed a limited number of animals (Spencer, 1955). Tevis (1956*a*) indicated that *Peromyscus* feed heavily on insects on a fresh burn.

In 1956, the experimental area did not appear to be good *Peromyscus* habitat; however, the deer mouse population was roughly twice as great as under virgin conditions. The control grid *Peromyscus* population tended to have its usual numbers and to follow its normal pattern.

Movements.—From October 11 to 14, just prior to the start of the burn on the 5B area, 16 *Peromyscus* were captured on the experimental grid. These animals will be referred to in the following discussion as the original population.

During October 16 to 23, while the fire was burning on the 5B area, ten (62.5 per cent) of the original animals were captured on the movement lines in the green timber. Some would have been in the timber under normal conditions but not in as great numbers. The fire apparently caused an increased movement to the timber. Under somewhat similar circumstances, Tevis (1956*b*) recovered 32 per cent of his marked *Peromyscus*.

The fire died down and trapping was resumed October 24 to 29 with eight (80 per cent)

of the movement line animals from the original population recaptured on the experimental grid. Four original animals not captured on the movement lines were also taken. Thus, within 15 days after the start of the burn, 12 (75 per cent) of the 16 original animals were recaptured on the experimental grid.

On November 11 to 14 the experimental grid was again trapped. At that time all ten of the original animals which were captured on the movement lines during the fire were taken. In addition, three of the original animals not caught on the movement lines were recaptured, making a total of 13 (81 per cent) of the original animals taken. These data reveal that deer mice have a very strong attachment to their homes. Murie and Murie (1932), reporting on a different subspecies of *Peromyscus*, found a similar attachment.

During the post-burning October and November checks of the experimental grid, 14 (87 per cent) of the original *Peromyscus* population were recaptured. It is normal for a mouse population to change its composition rapidly, and the loss of a few animals during a two-month period is to be expected. Therefore, the burn on the experimental area had little influence in reducing the number of *Peromyscus* in the original population.

Eleven of the 21 animals captured on the experimental grid after the fire were caught on the movement lines during the burn. Since 12 of the 21 animals on the grid after the fire were captured there prior to the burn, the data suggest that about 57 per cent of the post-burning population on the area was composed of former occupants. The data also revealed a regular movement of *Peromyscus* between the cutting and the timber.

A compilation was made of the maximum distance between capture sites of *Peromyscus* on the experimental grid and movement lines. The minimum possible capture distance was 300 feet and the maximum about 1,700 feet. The data indicated that 14, or 19.4 per cent, of the *Peromyscus* traveled from 601 to 700 feet between the experimental grid and the timbered movement lines. This mode for 72 travel distances is about twice the minimum. The movement range was 301 to 1,500 feet. The travels of adult male No. 2539 are of special interest. He was caught each month from July to November, 1956, in the same general vicinity on both the experimental grid and the movement lines. His maximum travel distances were 1,266, 1,254, 1,204, 1,154 and 1,410 feet, respectively.

The experimental grid was located in the cutting midway between the timber on the east and west sides. The *Peromyscus* seemed to travel to the nearest standing timber and to check on this the following compilation was made:

	Number	*Per cent*
Nearest timber	60	83.3
Equidistant timber	8	11.1
Farthest timber	4	5.6
Total	72	100.0

The data show a definite tendency for the *Peromyscus* to visit the nearest timber. If one includes half of the equidistant animals, the figure approaches 90 per cent.

Sex ratios and reproduction.—During the entire study period, 132 *Peromyscus* were captured on the experimental grid. Of this group, 74 were males and 58 females: a sex ratio of 56 per cent males, which is a greater spread than is found in many populations. The monthly captures were not large enough to justify sex ratio computations.

An effort was made to follow the breeding cycle of the live-trapped *Peromyscus* on the experimental grid. The criterion used for determining the breeding cycle for the males was the location of the testes. If they were descended and prominent, the animal was considered to be in breeding condition; if small and retracted, they were considered non-breeding. The breeding status of the females was based on the vulva condition, and whether or not the animal was lactating. Jameson (1953) found that a perforate vulva occurred during estrus and parturition, and was variable during gestation. Thus, a pregnant female might not have a perforate vulva but would be in its breeding cycle.

In 1954 the *Peromyscus* were breeding at a high rate on the experimental grid. In May, 1955, there was evidence of breeding; however, breeding was low in August after the area was logged. Low breeding activity continued after burning and through the last check in November. The data for 1956 revealed a high rate of breeding from May to November inclusive, similar to the 1954 breeding season.

A few *Peromyscus* litters are born in the live traps each year. In 1954 three litters were born in the experimental grid traps, none were found in 1955, but three were found in 1956.

The disturbance caused by felling, logging and burning seemed to disrupt the breeding activity on the experimental unit. Similar data from undisturbed populations of deer mice in the same general vicinity, however, also revealed a decided slump in the 1955 breeding after early spring. During the summer of 1955 the ground temperature was frequently above 150°F. and it was very dry. This may have been responsible for the lack of breeding activity. In any event, reproduction by resident animals was not a factor in the repopulation of the 5B cutting until the spring of 1956.

RED-BACKED VOLE (*Clethrionomys californicus obscurus*)

Populations.—Red-backed voles are not as hardy as *Peromyscus*, and several died in the traps in spite of an abundance of food and of wool from which they could have made a nest. Deer mice readily make nests of the wool, but only an occasional red-backed vole utilized it for that purpose. Most of them pulled the wool from the bar and trampled it into the urine and feces until it was a sodden mass. Efforts were made to tend the traps during late afternoon and early morning—this helped to reduce but did not eliminate losses. Because of this trap mortality, the population estimates should be considered minimum figures and accepted with reservations.

Generally speaking, the red-backed vole population was a little greater on the experimental than on the control grid during the time when both areas were in virgin condition. There was a low spring and early summer population with a gradual increase during fall and early winter. The population estimate in the old-growth Douglas-fir forest varied from 0.5 to 4.0 animals per acre depending on the season. Tevis (1956*a*) considered virgin coniferous forest to be the best habitat for these voles.

During 1954, the population ranged from 0.5 to 3.2 animals per acre. In May, 1955, it was estimated to be 2.0 animals per acre. Felling started in June, and it was not possible to trap again until August after logging had been completed on the grid. August trapping indicated a population of 2.2 animals per acre which was a little greater than the pre-felling May estimate. The population increased during September and reached its highest level of 5.0 animals per acre in early October just prior to the burn. The first post-burning population check during late October revealed 1.9 animals per acre—a loss of approximately three-fifths of the population from the pre-burning level. By November red-backed voles had increased to 3.0 animals per acre.

During 1956 the experimental grid was trapped for seven periods and no *Clethrionomys* were captured. From November, 1955, to May, 1956, the voles had either succumbed or moved from the area. The data suggest that felling and logging did not change the habitat enough to discourage them. Although the closed canopy was removed, enough cull logs and wood debris remained to give a closed canopy effect at ground level in a patch-wise pattern. However, burning changed the habitat drastically; many of the cull logs and debris were destroyed, thereby reducing or eliminating the closed canopy effect at ground level, and practically all the green vegetation was burned or killed. Since these voles are thought to subsist largely on vegetation, the fire probably eliminated both their food supply and their living quarters. In contrast, during 1956 the control grid displayed a relatively normal population level. Tevis (1956*a*) reported a somewhat similar experience on cutovers in northern California.

Movements.—Unlike *Peromyscus*, the red-backed voles did not reveal much movement.

Only three experimental grid animals were captured on the movement lines. These movements were all made during May, 1955, and were of 206, 226 and 470 feet. There was not much difference in the range length of *Clethrionomys* on the control and experimental grids, or between virgin and logged conditions. The combined range length of 65 animals for both grids and both types of habitat ranged from 50 to 300 feet and averaged 154 feet.

Eleven voles were captured and released on the experimental grid during May, 1955. Felling started on the area in June and it was not trapped again until August after the area was logged. At that time, five of the May animals were recaptured; thus, 45.4 per cent of the population persisted during the three-month felling and logging period. Since 5 of the 12 voles captured in August had also been taken in May, they formed 41.7 per cent of the August population. This is lower than the average turnover for an undisturbed population, and it appears that felling and logging caused very little if any mortality.

From October 11 to 14, 27 voles were captured on the experimental grid and released. None of these animals was caught on the movement lines while the area was burning. When the experimental grid was trapped after the fire, from October 24 to 29, ten voles were captured of which four had been taken just prior to the burn. Therefore, immediately after the fire 14.8 per cent of the pre-burning population were captured on the grid, and they comprised 40.0 per cent of the population.

The experimental grid was again trapped November 8 to 11 at which time ten voles were captured. Of this group, two had been taken prior to the fire and were caught for the first time since the burn. Consequently, it was known definitely that 6 or 22.2 per cent of the pre-burning voles survived the fire.

Previous data indicate that these voles do not travel as extensively as *Peromyscus*. Even when threatened by fire, they apparently stay within their normal ranges. It is thought that the animals surviving the burn stayed on the area during the fire and were fortunate enough to reside in an unburned spot or to have dens which protected them from the heat and smoke.

Sex ratios and reproduction.—Ninety-seven *Clethrionomys* were captured on the experimental grid during the study. Of this number, 54 were classed as males and 43 as females, a sex ratio of 100 males to 80 females.

The monthly breeding data for the experimental grid were based on small samples. However, the undisturbed 1954 breeding trends were comparable to those during 1955 when the timber was felled, logged, and the area was burned. The animals were breeding in April when the first spring population checks were made and continued until the first part of October. During late October and November there was a marked decline in breeding activity. The monthly breeding pattern on the control grid was similar to that on the experimental area. The data indicate that reproduction probably was an important factor in maintaining and building up the red-backed vole population on the experimental grid during the felling, logging, and immediate post-burning period.

Although breeding started in early spring, its effect on the population was not pronounced until August or September. This delayed build-up is thought to be due to natural deaths of over-wintering animals. Thus, the early young of the year would not increase the population but would only be replacements. Since it would take some time for them to reach maturity and produce young, the population increase would be delayed. One other possibility which might explain the delayed build-up is trap mortality. Both factors probably operated together on the population in the present study.

CHIPMUNK (*Eutamias townsendi cooperi*)

Populations.—The chipmunk populations on the control and experimental grids were 2.2 and 2.1 animals per acre, respectively, during late fall, 1954. By fall of 1955, the control grid was still in virgin condition and had an estimated 2.3 chipmunks per acre. The experimental grid had been cut and logged, and the estimated density had dropped to 1.7 animals per acre. In the fall of 1956 the control grid had an estimated 3.8 chipmunks per

acre compared to 0.5 per acre on the logged and burned experimental grid. The west movement line grid was also trapped; it had a population of 1.4 chipmunks per acre, which was considerably lower than the population on the control grid.

The data show that chipmunk populations varied from 1.4 to 3.8 animals per acre under virgin forest conditions. The first year after logging and burning there were only 0.5 chipmunks per acre on the experimental grid. They must increase rapidly, however, since Tevis (*1956a*) indicated that cutovers 3 to 10 years old will have from two to four times as many Townsend chipmunks as virgin forest.

Movements.—Twenty-three range lengths were secured for chipmunks frequenting the control, experimental, and west movement line grids. All were obtained under virgin forest conditions and averaged 302 feet.

A compilation was made of the distance between the capture site of each chipmunk on the small experimental grid and the movement lines. The minimum possible travel distance was 300 feet and the maximum about 1,700 feet. The chipmunks ranged from 401 to 1,300 feet; the mode was from 501 to 600 feet.

In October, 1955, just prior to the burn, 50 per cent of the experimental chipmunks were trapped on the movement lines. Eighty per cent of the post-burning chipmunks were captured on the movement lines while the fire was burning on the experimental area. The percentage of experimental grid chipmunks captured on the movement lines varied from 33.3 to 66.7 per cent during 1956.

The data indicate that chipmunks can travel relatively long distances in a short time. While trapping, the impression was gained that burning caused the chipmunks to leave the cutting unit for the timber, and the trapping data support this impression. The chipmunks apparently ranged from the timber onto the cutting but did not reside there the first year after the burn.

Sex ratios and reproduction.—Logging reduced the number of chipmunks on the experimental grid but not so drastically as did the fire. Because of these influences the total capture was much lower than it would have been under undisturbed conditions. Altogether 85 chipmunks were caught on the experimental grid. This sample of 52 males and 33 females gave a sex ratio of 100 males : 63 females, which is a greater spread than one would normally expect.

The breeding data do not reveal any fluctuation which could be attributed to felling, logging and burning the experimental area. Chipmunks breed in early spring, about the time they emerge from hibernation, and their breeding was probably over before the logging activities started. Nestling chipmunks could have been killed by the logging operations but the study was not thorough enough to detect such mortality.

OTHER SPECIES

Oregon vole, Microtus oregoni.—There was a light population of these voles in the virgin forest of the study area. None was captured on the experimental grid during 1954 and 1955; however, one was caught in July and another in August, 1956. Two individuals were tagged in September and three in October of the same year. Although vegetation was very sparse on the cutting during 1956, Oregon voles were seemingly attracted, at least temporarily, to this recently logged and burned area.

Trowbridge shrew, Sorex trowbridgei.—Trowbridge shrews were occasionally captured in the virgin forest, although none was taken on the experimental grid prior to logging. After felling and logging, six of these shrews were caught on the area. Two were captured after the unit was burned in October, 1955, and two were taken in October, 1956. All except one of these animals died in the traps, and it was not recaptured. The trap mortality makes it difficult to evaluate the effect of logging on the Trowbridge shrews; however, the meager data suggest they may have been attracted, at least temporarily, to the area.

Vagrant shrew, Sorex vagrans.—Vagrant shrews were caught less often in the virgin forest

than Trowbridge shrews. Only one was taken on the experimental grid, and that was during September, 1955, after the area had been logged.

Chickaree, Tamiasciurus douglasi.—Chickarees were relatively common in the virgin forest, but no captures were made during the study. After the 5B unit was logged, they were not seen on the cuting but were observed in the timber near its edge. Logging apparently ruined the area as a habitat for them.

Flying squirrel, Glaucomys sabrinus.—An occasional flying squirrel was captured in the virgin timber; none was caught on the experimental grid, and it seems logical to assume that logging destroyed their habitat.

Short-tailed weasel, Mustela erminea.—These small weasels were occasionally captured in the virgin forest. None was caught on the experimental grid prior to logging; however, two were taken after logging, but prior to burning. The increased deer mouse population may have attracted them to the area.

Bushy-tailed wood rat, Neotoma cinerea.—Bushy-tailed wood rats were not trapped in the virgin forest. None was captured on the experimental grid until after the area had been logged when one was taken. It does not seem that cutting attracted the animal since there are no rock or ledge habitats nearby. It is thought the animal was wandering around and just happened onto the area. Bailey (1936) indicates that wood rats often appear at places which are long distances from their preferred habitat.

Pika, Ochotona princeps.—Only one pika was captured during the study; it was taken on the experimental grid after logging. The animal probably wandered to the area and was not attracted by the cutting.

Snowshoe hare, Lepus americanus.—A few snowshoe hares were noted in the virgin forest. Neither the hares nor their sign were observed in the clearcut the first year after logging. Freshly burned clearcuts are poor hare habitat but older, brushy cuttings are desirable.

SUMMARY AND CONCLUSIONS

The estimated deer mouse population ranged from 0.0 to 2.5 animals per acre in old-growth Douglas-fir. There was an increase in the population after felling and logging. Burning caused many *Peromyscus* to go to the nearest green timber; after the fire they returned to their homes. Shortly after the fire the density was two to three times that of the virgin timber population. The following year the deer mouse population was about twice its virgin timber level. *Peromyscus* regularly traveled between the clearcut and the timber—some individuals ranged about one-fourth mile. Breeding of resident deer mice was not an important factor in the repopulation of the cutting unit immediately after the fire.

Because of trap mortality the red-backed vole population estimates are considered to be minimum figures. The virgin timber population ranged from 0.5 to 4.0 animals per acre. They increased on the experimental grid after logging but decreased sharply after the burn, only to increase again before winter. None was captured on the experimental grid the first season after it was burned. These voles apparently remained on the area during the fire. Breeding was thought to be an important factor in maintaining and building up the population during felling, logging and the immediate post-burning period.

It was estimated there were from 1.4 to 3.8 chipmunks per acre in the virgin timber. Logging caused a modest reduction in abundance on the experimental area. The first year after burning, it was estimated there were 0.5 animals per acre. Many chipmunks moved to the forest when the cutover was burned. They apparently ranged from the timber onto the burn the first season after the fire but did not reside there.

Oregon voles, short-tailed weasels, Trowbridge shrews, vagrant shrew, bushy-tailed wood rat and pika were captured on the clearcut after logging. Chickarees, flying squirrels and snowshoe hares were neither captured nor observed on the area after logging.

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U.S. Fish and Wildlife Service, Oregon State College, Corvallis. Received July 3, 1957.

A METHOD OF LIVE-TRAPPING SMALL TAIGA MAMMALS IN WINTER

BY WILLIAM O. PRUITT, JR.

The numbers of live-trapping studies of small mammals are legion and more are begun and completed every year. Almost invariably these studies are carried out during the snow-free seasons of the year. So traditional has this practice become that the snow-free part of the year is usually known as the "field season."

For temperate regions this concentration of effort on the snow-free period may be excused on two grounds: (1) the period of snow cover is unpredictable and intermittent and (2) the snow cover seldom achieves a thickness that is usable by the field naturalist.

For large regions of the earth, however, a snow cover forms in the fall and remains until spring. In these regions the field naturalist must know something about the activities of the small mammals during the period of snow cover. In the taiga of interior Alaska this period of subnivean activity usually

lasts from middle or late October until early or middle May. This is over half the year. For small mammals with a comparatively short life span one cannot afford to ignore such a significant portion of it. Not only is the presence of a stable snow cover itself the major factor that has allowed small mammals to ecize the taiga, but the temporal and spatial variations in the snow cover and in its morphology are powerful forces which mold and shape the size, distribution and behavior of small mammal populations in the taiga (Formosov, 1946). One cannot say that he knows the small mammals of the north country until he knows their subnivean activity.

Any attempt to study the winter activity of mammals under soft, fluffy taiga snow immediately runs into several practical difficulties. The human organism itself, being a tropical primate, must make numerous adjustments in clothing, equipment and behavior patterns. Next comes the realization that a two-footed creature lumbering through a snow cover effectively alters that snow cover not only for the present and immediate future but for the remainder of the winter as well. Finally, there is the problem of contact between the investigator and the animals.

It would be possible to tag the animals with a radioactive tracer and track them with an instrument sensitive to the radiations (Godfrey, 1954, 1955; Karlstrom, 1957). There are a number of practical difficulties connected with this method, not the least of which is the cost. Moreover, there still remains the problem of the initial contact with the animals.

An alternate approach to the problem is to find or make some sort of contact tunnels into the subnivean habitat of the animals. I fully realize that this method disturbs the habitat somewhat, but any insight into the lives of the animals, even though partly disturbed, is better than no information at all. Continued presence of well-weathered trap chimneys, as used in this study, probably disturbs the animals' activities no more than does the introduction of live traps into any habitat.

A number of chimneys 7½ × 12 × 45 inches, with hinged lids, were made out of ⅝-inch plywood (Fig. 1) and were screwed to stakes which had been driven into the ground at regular intervals on a study plot. One side of the chimney was 4 inches shorter at the bottom than the other three. The chimneys were so placed that the three long sides were below the moss surface and the short side slightly above it. This allowed surface entrance to the chimney while preventing snow from completely filling the base. The anticipated thickness of the snow cover governs the height of the chimneys. These chimneys were put in place in the summer and allowed to become thoroughly weathered. In the fall the interiors of the chimney bases were prebaited with a supply of oat flakes.

In order to disturb the snow cover as little as possible, only one continuous snowshoe trail was made from trap to trap. Preservation of the fragile, lattice-like layer of depth hoar or *púkak* is necessary so that free movement of the animals is not hindered. Previous investigations had revealed that when a

snow cover averaging 0.2 gm./cm.^{3} reached a thickness of over 60 cm., it would support a carefully made snowshoe trail without collapse of the púkak. In the winter of 1955–56 this thickness occurred by January. The *Clethrionomys rutilus* population on the area unfortunately was so low that too few captures were made to enable one to judge the method. During the winter of 1956–57 the snow cover again reached the 60-cm. critical thickness by January and the vole population was sufficiently high to enable a number of captures to be made.

The voles were caught in masonite live traps which fitted inside the chimneys. Two 5/8-inch cup hooks were screwed into the top of each trap. A piece of welding rod was bent into a hook and used to engage the cup hooks and thus raise and lower the traps so that they could be checked for captures.

With ambient temperatures of –30°F. or thereabouts the traps had to be checked at least every eight hours. The only voles lost were those left in the traps for ten hours. As I have shown elsewhere (Pruitt, 1957) even with ambient temperatures of –20 or –30° the subnivean temperatures are on the

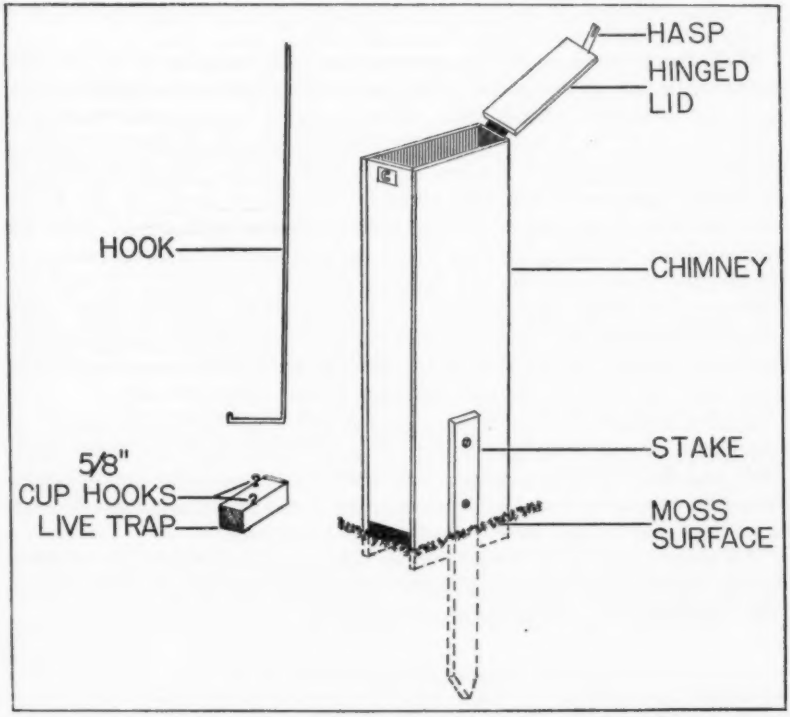

FIG. 1.—Details of equipment needed for subnivean live-trapping.

order of +10 to +30°F. I have had up to ten recaptures of one vole, all at ambient temperatures of 0°F. or lower.

No nesting material was used in the traps. Experience has shown that at temperatures consistently below freezing the animals' urine freezes in the nesting material and creates problems such as jamming of the door or treadle. The traps were kept heavily stocked with oat flakes. I feel that a supply of food in the traps and constant attention so that no animal remains in the traps too long is better than relying on nesting material for survival of the animals.

Equipment needed for checking the traps consisted of a plastic bag of oat flakes for replenishing the bait, the hook for pulling up the traps, a pack of 3 × 5 record form cards, scissors for clipping toes, a small cloth sugar sack for receiving the animals from the traps, a screwdriver and a Coleman lantern. A screwdriver is very useful for emergency repairs and adjustments of balky trap treadles and for cleaning frost from the treadle, door and trigger mechanism. I have found that about 60 or 70 traps may be handled per hour.

It is obvious that the use of these chimneys is possible only in the taiga, not the tundra. Winds strong enough to cause frequent drifting of the snow also cause the formation of hollows or *aŋmaŋa* around the chimneys, thus nullifying their usefulness.

While this paper is primarily a presentation and discussion of this trapping technique, a few very tentative preliminary results from one application of it might be mentioned as indicative of the types of investigations that could profitably use it. As is well known, the taiga snow cover is quite irregular in thickness because of the "shadow effect" of the trees. These bowl-shaped depressions underneath the limb cover of spruces are known to the Kobuk Valley Eskimo as *qámaniq*. I have shown elsewhere (Pruitt, *op. cit.*) that the thermal regime of the forest floor under the qámaniq is colder and has more fluctuations than under the full snow cover. It is interesting to note that *Clethrionomys rutilus* appeared to avoid the areas of qámaniq—their home ranges had vacuoles, as it were, which were qámaniq. Indeed, it appeared that the voles used to a greater extent the parts of their home ranges where the snow cover was thickest (in this particular winter, up to 100 cm.).

Another tentative result was the apparent lack of a diel rhythm in activity. Considering the lack of light in the voles' subnivean habitat (Bader *et al.*, 1954) and their infrequent surface excursions, this is not surprising. Likewise, during the summer, when the Fairbanks region receives approximately 22 hours of sunlight daily, a diel activity rhythm appears lacking.

This paper results from research which was supported by the U.S. Air Force through the Office of Scientific Research and by the Department of Physiology, School of Medicine, University of Pennsylvania.

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Box 282, College, Alaska. Received August 30, 1957.

GENERAL NOTES

THE CORRECT NAME OF THE OLIVE BABOON

There is, at present, much unnecessary confusion regarding the correct scientific name of the olive or Anubis baboon, known to nineteenth century zoologists as *Papio* or *Cynocephalus anubis*, but nowadays referred to most commonly as *P. doguera* Pucheran, 1856 (e.g., Fiedler, 1956) on the assumption that *anubis* Fischer, 1829 (based on a plate of F. Cuvier) is indeterminable.

The first description of an animal of this species was that of F. Cuvier (1824*) who, at that date, was in charge of the menagerie at the Jardin des Plantes, where his living model resided. His description is accompanied by an excellent plate of an obviously adult male judging from the size of the scrotum and general physique of the animal. The work in which the account was published appeared in livraisons, each entitled with a gallicised name of the species concerned, the present subject being headed *Cynocéphale anubis*. Some have doubtless felt that this was not a binomial term in the Linnaean sense and accordingly the name *anubis* is quoted as deriving from Fischer's *Simia anubis* of 1829—which was, as already stated, based on Cuvier's earlier publication. But Cuvier's *anubis* can be validated as a scientific name by virtue of the fact that in the Table générale et méthodique at the beginning of his folio work the title of the subsequent livraison is referred to binomially as *Cynocephalus anubis* (No. 50).

Whatever the imperfections of the description, the plate is so clear as to leave no doubt in the mind what animal it is intended to depict.

Pocock (1925) summed up the position in the following words: "It is almost incredible that the commonly imported, large dark green baboon referred to in a previous paragraph as the species considered by Elliot (1913) as *Papio nigeriae* was unknown to zoologists of the first half of the 19th. century and in my opinion those who assigned the name *anubis* to it were perfectly justified. It is true that Cuvier's type of *anubis* is lost and was unlocalized. Probably it was a specimen living in the Jardin des Plantes and was not preserved when it died. But the figure and description of it apply so closely to the West African species above referred to as to warrant the adoption for this species of that name which has long been assigned to it by tradition."

* This is the date given on the title page of the copy in the Zoological Society's Library, but the article itself is dated June, 1825. Sherborn gives 1842 as the date of *anubis* Geoffroy and Cuvier. This, doubtless, relates to a quarto edition, of which there were presumably several. One in the writer's possession is dated 1833: here the *anubis* is depicted on Plate 43 and described on pp. 125–127.

J. A. Allen (1925), writing about the same time (presumably a little earlier as Pocock quotes him), on the contrary considered *anubis* to be "absolutely indeterminable." Allen's grounds for this were (1) the juvenility of the "type" (an erroneous deduction); (2) equivocality of original description and plate (also erroneous) whereby the type locality had variously been ascribed to both East and West Africa by successive authors. He quoted Anderson (1902), for example, who "assumed on wholly conjectural grounds that the type probably came from the Upper Nile valley." Ogilby (1838) considered it a Nubian species, but later (1843) changed his opinion, assigning it to West Africa.

J. A. Allen was followed in his views by G. M. Allen (1939) who, in his checklist, adopted *P. doguera* for the olive baboon.

The only recent writers who subscribe to Pocock's opinion are Swynnerton and Hayman (1951: 299 fn.) who state that "it appears to us that *P. anubis* is a valid name as it was based on a full description and good coloured plate of the 'Anubis' in Geoffroy and Cuvier's *Histoire naturelle des Mammifères* (vol. 3, livr. 50, June, 1825)."

Accordingly, it is hereby submitted that *Papio anubis* F. Cuvier is the correct name for the olive or Anubis baboon, and the type locality restricted as of Ogilby (1843) and of Pocock (1925) to "West Africa." The East African race will therefore become *P. a. doguera* Pucheran, other races of possible validity being *P. a. neumanni* Matschie, *P. a. tesselatus* Elliot and *P. a. heuglini* Matschie.

A word in conclusion is necessary relative to *Cynocephalus olivaceus* I. Geoffroy, 1848. This turns out not to be a synonym of *anubis*, but of *P. papio* (Desmarest) as suspected by Elliot—despite the unlikelihood of Geoffroy's adopting this specific name for a reddish animal. The type, a juvenile male from "Avory, Golfe de Benin" given by M. Cabarret, lieutenant de vaisseau, died in the Paris menagerie in September, 1847. Its skin is still extant in the Paris Museum (Rode, 1938) and has been recently examined, at my request, by my friend M. Pierre Dandelot, who has discussed its identity with Messrs. Dorst and Petter of the Paris Museum, all of whom concur that the animal is *P. papio*. I am very grateful to these gentlemen for this service and to M. Dandelot especially for his excellent colored sketches of the type specimen.—W. C. Osman Hill.

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Dept. of Anatomy, Emory Univ., Georgia. Received October 11, 1957.

SUBSTITUTE NAME FOR *LEPUS AMERICANUS SECLUSUS* BAKER AND HANKINS

Henry W. Setzer has kindly called my attention to the fact that *Lepus americanus seclusus* Baker and Hankins (Proc. Biol. Soc. Washington, 63: 63, May 25, 1950) is preoccupied by *Lepus timidus seclusus* Degerbøl, 1940. As a substitute, I propose *Lepus americanus setzeri*. —ROLLIN H. BAKER, *The Museum, Michigan State University, East Lansing. Received October 10, 1958.*

MELANISTIC GROUND SQUIRRELS FROM OHIO

On June 16, 1954, Mr. Clyde B. King brought to the Ohio State Museum a live black ground squirrel, *Citellus t. tridecemlineatus*. The specimen was caught by Burdette King on June 11, 1954, at the Mound City Group National Monument, about 3 miles north of Chillicothe, Ross County, Ohio. It was preserved as No. 1846 in the Ohio State Museum collection of mammals. According to King, this is the second specimen found at this locality, the first having been taken two years previously and presented to Karl Maslowski of Cincinnati, Ohio.

On August 30, 1954, a third specimen was presented to the Ohio State Museum (OSM No. 1898) by Burdette King. This was taken alive on July 2, 1954, at the same locality. Both specimens are black above. The feet and underparts are covered with a mixture of black and white hairs, resulting in a gray appearance.

This colony of ground squirrels was under observation by the writer daily during the summer of 1941, but no black specimens were observed. The colony is heavily populated and many specimens may be observed there during the summer months.

King mentions that one or two black specimens have been seen at regular intervals at the south end of the Veterans Hospital grounds near Mound City, and that one farmer reports having seen black specimens on his farm near Yellow Bud, which is about 10 miles north of Mound City.—ROBERT M. GOSLIN, *Ohio State Museum, Columbus 10, Ohio. Received October 31, 1957.*

THE BAILEY POCKET MOUSE IN NEW MEXICO

Specimens of *Perognathus baileyi baileyi* Merriam in the University of New Mexico Collection of Vertebrates from three localities in the Peloncillo Mountains, Hidalgo County, New Mexico, provide the first records of the occurrence of this species in the state.

On August 22 and 23, 1956, I obtained four *P. baileyi* in Guadalupe Canyon, Peloncillo Mountains, at approximately 4,500 feet, 31 miles south of Rodeo, Hidalgo County, New Mexico. These specimens were taken on the mesquite-covered rocky slopes of the canyon. Owl pellets picked up on August 21, 1956, in Skeleton Canyon, approximately 4,900 feet, 10 miles south of Rodeo, Hidalgo County, contained the remains of at least four *P. baileyi*. On January 30, 1957, a field party from the University of New Mexico Biology Department obtained an additional specimen of this mouse at the crest of the Peloncillo Mountains on the Geronimo Trail at an approximate altitude of 5,900 feet, 21 miles south of Rodeo. The latter animal was captured in a community of beargrass (*Nolina microcarpa*), *Yucca* sp., annual grasses, alligator juniper (*Juniperus pachyphloea*) and century plant (*Agave* sp.).

The taking of these specimens provides a range extension southeastward from the Graham Mountains, Graham County, Arizona (Hoffmeister, Amer. Midl. Nat., 55: 278, 1956) of approximately 82 miles. *Perognathus baileyi* is not known to occur in northeastern Sonora or in southeastern Arizona. The present records point to the likelihood of its occurrence in these areas.—JAMES S. FINDLEY, *Dept. of Biology, Univ. of New Mexico, Albuquerque. Received October 16, 1957.*

FIRST RECORD OF THE PIGMY MOUSE IN NEW MEXICO

On April 6, 1956, two pigmy mice, *Baiomys taylori*, were collected 18 miles south and 2 miles west of Animas, Hidalgo County, New Mexico. These two specimens, both adult females (74131, 74132 KU), provide the first record of occurrence of pigmy mice in New Mexico. To my knowledge, the nearest localities of record to the New Mexico station are 5 to 9 miles west of Hereford, Cochise County, Arizona, and 5 miles southeast of Chihuahua City, Chihuahua, Mexico (see Burt and Blossom, Occas. Papers Mus. Zool., Univ. Michigan, 465: 1–4, 1942), and Casas Grandes, Chihuahua (see Osgood, N. Amer. Fauna 28: 256, 1909). It is worthy of note that the pigmy mice from Arizona were newly described by Burt and Blossom (*loc. cit.*) as *Baiomys taylori ater*, whereas specimens from near Chihuahua City were assigned by them to *Baiomys taylori paulus* (previously described by J. A. Allen in 1903 from Río Sestín, Durango).

The two specimens from New Mexico have been compared by me with paratypes of both *B. t. ater* and *B. t. paulus*. From *B. t. ater* they differ in being Olive-Brown instead of Cinnamon-Brown dorsally, and Smoke-Gray instead of Cinnamon-Buff ventrally; in cranial characters there are no appreciable differences. *Baiomys t. paulus* differs from the New Mexican specimens in being Buffy Brown dorsally, and Pale Olive-Buff ventrally (color terms are those of Ridgway, Color Standards and Color Nomenclature, Washington, D.C., 1912) and in having a narrower interorbital region and narrower anterior part of the zygomatic arch. Because the specimens from New Mexico resemble *B. t. ater* in characters of the cranium, I tentatively assign them to that subspecies.

Measurements (in mm.) of the two specimens from New Mexico are as follows: total length, 105, 107; length of tail vertebrae, 43, 43; length of body, 62, 63; length of hind foot, 14, 14; length of ear from notch, 10, 11; occipitonasal length, 17.7, 17.8; least interorbital constriction, 3.5, 3.6; zygomatic breadth, 9.4, 9.6; depth of cranium, 6.4, 6.4; breadth of cranium, 8.7, 8.7; alveolar length of maxillary tooth-row, 3.2, 3.3; postpalatal length, 6.2, 6.2; length of incisive foramina, 4.0, 4.0; length of rostrum, 5.8, 6.1.

The pigmy mice from New Mexico were trapped in the runways of cotton rats, *Sigmodon minimus*, in the grasses and weeds.

Since this paper was transmitted, Justice (Jour. Mamm., 38: 521, 1957) has recorded pigmy mice from Cochise County southeast of Chiricahua, Arizona, at a place (or places) 5 to 20 miles north of the Mexican border—only 35 to 40 miles southeast of my record station in Hidalgo County.

I am grateful to George G. Goodwin, the American Museum of Natural History, and William H. Burt, Museum of Zoology, University of Michigan, for permission to examine paratypes herein discussed.—Robert L. Packard, *Museum of Natural History, University of Kansas, Lawrence.* *Received November 22, 1957.*

A NEW TEXAS LOCALITY FOR *DIPODOMYS ORDI*

The known range of *Dipodomys ordi sennetti* (J. A. Allen) in Texas has been reported as southern Texas, south of Corpus Christi and northwest to Somerset in Atascosa County (Setzer, Univ. Kansas Publ. Mus. Nat. Hist., 1(23): 517, 1949).

On August 19, 1957, I collected an adult male of this form crossing State Highway 80, 2 miles north of Nixon in Gonzales County. The skin and skeleton have been deposited at the University of Texas, TNHC No. 5069. This record extends the known range of the species 55 miles east of the previously known northeastern limits in Texas.

The surface outcrops in this area are of the Eocene Claiborne group. Most of the formations of this group produce a deep sandy soil which supports, for the most part, a post oak–blackjack oak association. These sandy soils extend in arcuate belts from Atascosa County northeastward, roughly paralleling the Balcones escarpment, and furnish a ready avenue of dispersal for *Dipodomys*.

It would not be unreasonable to expect that extensive trapping in this region would show a somewhat wider range than has been previously reported.—GERALD G. RAUN, *Dept. of Zoology, Univ. of Texas, Austin. Received November 19, 1957.*

SEA OTTER ALONG THE CALIFORNIA COAST

There have been reports of fishermen seeing sea otter, *Enhydra lutris*, in coastal waters near Trinidad, Humboldt County, California, but none of these observations have been verified by mammalogists.

On December 1, 1956, I noted two mammals in the ocean just south of the kelp beds which extend from the mouth of the Little River to the vicinity of Trinidad Head. These mammals were observed at close range by flying over them; they were identified as sea otter floating on their backs and their light-colored heads were distinctive from their darker bodies. The animals were about one-fourth mile from shore.

Observations made in this area through the spring months of 1957 did not reveal their presence, but it is hoped that these otter are utilizing the extensive kelp beds that occur along the shores of Humboldt and Del Norte counties, and that a population of sea otter will build up along this coastal area.—WALLACE W. BENTLEY, *Humboldt State College, Arcata, California. Received October 16, 1957.*

UNUSUAL CAPTURE OF A BADGER

Early in August, 1918, a friend, Mr. Harry Saunders, who lived on his ranch at Hillsdale about 5 miles southeast of El Cajon, San Diego County, California, complained to me that coyotes were catching his chickens and requested the loan of a steel trap.

As a result a No. 1½ single-spring Newhouse trap with verbal instructions for proper setting to catch coyotes, was given him. The trap had a 6-foot length of chain attached to allow it to be set in an open space away from a bush or an object close to which a coyote would not venture.

Several weeks passed without hearing from Mr. Saunders. Then, on September 27, he telephoned informing me that a badger was in the trap. Arriving at the ranch I found that a full-grown badger, *Taxidea taxus*, had been captured and from the appearance of the trap site, had been in the trap several days.

In all my experience with trapped badgers, the victims had always done considerable digging, especially, if any length of chain permitted them to move. With this badger, who could move about with over 8 feet of free chain, there had been no digging whatsoever. The trap had been securely fastened at ground level to a corner fence post with this long chain and the animal had swept a circular area clean and smooth, 15 feet in diameter around the post, but not one claw mark had been made in the surface of the soil.

Further examination revealed all four feet were free. The spring of the trap was visible, extending beyond his tail, but the jaws were concealed. There was very little life in the poor creature as, when approached, he offered no resistance and would neither snarl, hiss nor blow. Usually a badger is very ferocious when caught in a trap.

I had no trouble in placing a fence post across his back above the lungs and stepping onto it, thereby crushing out his respiration. Death came quickly.

On turning the dead badger over I was astonished to find that the trap had gripped his scrotum close to the abdomen; both testicles were inside the jaws of the trap, uncrushed—an extremely torturous situation. Little wonder his viciousness had passed!

Immediately two questions were presented. Just how did this animal get into such a situation? And what habit or habits would cause it?

Upon analyzing the trap site, several factors were noted. As this fence corner was on a game trail, every varmint that traveled through the area naturally passed the spot. This fact, however, was unknown to Mr. Saunders when he set the trap. The trap had not been properly set to catch coyotes; it was just opened and placed on the ground with no attempt

at concealment or bedding. A dead chicken had been hung on top of the 6-foot fence post to which the trap was fastened—too high for an animal to reach—and maggots had eaten the bait, leaving only a desiccated, dried carcass that had a very, very dead smell.

This had attracted the attention of passing coyotes, though not to eat. They had also found the trap and, as their well-known canid habit, had urinated and defecated on it. A dozen dried scats on the perimeter of the large circle swept clean by the trapped badger gave proof of this. The coyotes' extremely cautious nature and keen sense of smell had kept them out of danger from the trap though they all had expressed their contempt for the place.

The badger, not being as cautious or as trap-wise as the coyotes, had in all probability been prompted to imitate the coyotes and stopped to defecate, unfortunately for him directly on the trigger pan of the open trap!

This specimen is now No. F 80 in the Dickey collection.—LAURENCE M. HUEY, *San Diego Society of Natural History, Balboa Park, San Diego, California.* *Received November 18, 1957.*

A LATE BREEDING RECORD OF A BOBCAT IN MASSACHUSETTS

Earlier workers who have studied the bobcat, *Lynx rufus*, in the Northeast (Seton, Lives of game animals, 1929; Hamilton, Mammals of eastern United States, 1942) state that the breeding season starts in late February and extends into March. Pollack (Jour. Mamm., 31: 327–330, 1950) suggests evidence that occasionally bobcats in the Northeast may breed as late as May and even June.

On October 29, 1957, Zebulon Jeffreys and Winfield Chambers shot three young cats while hunting rabbits in Shutesbury, Massachusetts. I examined and weighed these kits. The one male and two females averaged 3.2 pounds. The stomachs only contained yellow fluid, and the milk dentition was intact. It is believed these kits were still nursing. Their age was estimated as 12 weeks at most. Although there is no certain knowledge of the gestation period of the bobcat, estimates average 60 days. This suggests that the parents of these bobcats bred in the first week of June and the young were born in the first week of August.

This is a contribution of the Massachusetts Cooperative Wildlife Research Unit supported by the U.S. Fish and Wildlife Service, University of Massachusetts, Massachusetts Division of Fisheries and Game and the Wildlife Management Institute.—WILLIAM G. SHELDON, *Dept. of Forestry and Wildlife Management, Univ. of Massachusetts, Amherst.* *Received November 29, 1957.*

ADDITIONAL MULE DEER RECORDS FOR IOWA

The known range of the mule deer, *Odocoileus hemionus*, was extended to Iowa in 1954 when Sanderson reported a deer of this species killed near Leon, Decatur County (Jour. Mamm., 37: 457–458, 1956). Two additional records of mule deer in Iowa recently have been obtained.

During the 1955 deer season, William Stanton, of Hamburg, Iowa, shot with bow and arrow a male deer which he identified as belonging to this species. He killed the deer on an island of the Missouri River 4½ miles west and 1 mile north of Hamburg, Fremont County. Mr. Stanton reportedly killed the deer on flat terrain in heavy brushy cover. Associated with it were at least three white-tailed deer, *Odocoileus virginianus*. The antlers and portions of the skin were inspected by Elden Stempel, Biologist for the Iowa Conservation Commission, who photographed the deer. The photographs were sent to Dr. A. Starker Leopold who identified as a mule deer the specimen depicted.

Another male mule deer was killed during the 1956 season by Leonard Unterberg, a farmer who lives near Larchwood, Iowa. He killed the animal near the Big Sioux River in the NW ¼ of Sec. 25, T. 100 N, R. 49 W, in Lyon County on December 8, 1956. Topography of this area is rolling. Brushy cover is not especially abundant. Mr. Unterberg took the head antlers from the deer to a taxidermist at Sioux Falls, South Dakota, who recognized the species. After learning the identity of the animal, Mr. Unterberg contacted the Iowa

Conservation Commission. The antlers, hide and legs, examined by the writer, unquestionably were from a mule deer. The antlers were dichotomously branched; the tail white, with a black tip; and the metatarsal glands were 102 mm. long—larger than normal for white-tailed deer. Skulls from neither deer could be obtained for further inspection.

These two deer were taken at widely separate localities. Fremont County lies in extreme southwestern Iowa, Lyon County in the northwesternmost corner of the state. Together with Sanderson's report (*op. cit.*) of a mule deer from Decatur County (south-central), we can speculate that the species is widely scattered in Iowa.

The author wishes to thank Elden Stempel who supplied all information concerning the deer killed in Fremont County.—PAUL D. KLINE, *Iowa Conservation Commission, 711 A Ave., Vinton, Iowa.* *Received October 29, 1957.*

FURTHER STUDIES ON THE FEEDING EFFICIENCY OF BATS

An evaluation of the hypothesis that bats use their high frequency sounds for locating and pursuing flying insects (Griffin, Jour. Exp. Zool., 123: 435–466, 1953) has been made by the qualitative and quantitative analyses of bat stomachs (Gould, Jour. Mamm., 36: 399–407, 1955) as measures of the feeding efficiency of insectivorous bats. A conservative estimate was that about 500 insects were captured per hour by *Myotis lucifugus*. A random process of feeding cannot account for such high rates of catching insects. The number of dives per unit time of feeding bats has recently been observed to supplement the evidence based on stomach analysis. The study was made at the edge of a small swale on the outskirts of Baltimore, Maryland, during the summer of 1957. The bats were almost certainly *Myotis lucifugus* because of their size and manner of flight.

TABLE 1.—*Rates of diving by Myotis lucifugus in pursuit of insects, on the evening of July 7*

DURATION OF OBSERVATION, SECONDS	NO. OF DIVES OBSERVED	RATE: NO. OF DIVES/HR.
30	12	1,440
5	4	2,880
20	11	1,980
15	6	1,440
30	13	1,560
20	9	1,620
15	13	3,120*
140	53	1,363
5	2	1,440
33	6	655
10	8	2,880
15	3	720
20	3	540*
Total = 358	Total = 143	$\bar{x}$ = 1,665

*Range.

The dives were counted from the moment a bat came into view until it disappeared and, for convenience, this time will be called the "period of observation." The number of bats observed during any one evening varied from two to five. There was no way of knowing whether the same bat was being observed from one period of observation to the next. Table 1 lists all of the data collected on one favorable night (July 7) in the same order that the dives were observed. Table 2 is a compilation of data from several evenings. The total time in all periods of observation was 2,369 seconds and the total number of dives was 878.

TABLE 2.—*Diving rates of Myotis lucifugus*

DATE	MEAN NO. OF DIVES/HR.	RANGE OF DIVES/HR.	NO. OF OBSERVATIONS
30 June	792	540–1,260	10
3 July	726	360*–1,234	6
4 July	634	432–720	5
5 July	1320	960–1,800	4
6 July	1015	720–1,680	5
7 July	1665	540–2,880*	13
16 July	1263	747–1,938	8
18 July	1196	600–2,160	21
19 July	1437	900–2,250	24
31 July	1327	600–1,800	10
6 August	1369	720–2,160	11
	$\bar{x} = 1159$		Total = 117

*Range.

Four big brown bats, *Eptesicus fuscus*, were observed in the same way on the evening of July 10, at another site not far from the swale described above. Fourteen periods of observation were recorded, totaling 7 minutes. The mean number of dives per hour for all observations was 1,283 and the range of rates for each period of observation was 480–1,800 dives per hour.

Even if it were assumed that 50 per cent of the observed dives by *Myotis lucifugus* were *misses*, half of the impressive mean, 1,159 dives per hour (Table 2) would still come very close to the estimate, obtained through stomach analysis, of 500 insects caught per hour. These data seem to support the hypothesis that insectivorous bats capture flying insects by echolocation.

Helpful suggestions and review of the manuscript by Drs. Fred R. Cagle and Donald R. Griffin are deeply appreciated.—EDWIN GOULD, *Dept. of Zoology, Tulane Univ., New Orleans, Louisiana.* *Received November 14, 1957.*

Make your plans now to attend the meetings and participate in the program of the Society at Washington next June. Details on p. 164.

REVIEWS

Siivonen, Lauri. SUURI NISÄKÄSKIRJA. (Great Book of Mammals.) Otava Publishing Co., Helsinki. 800 pp., illus. 1956. Price, 3400 Finnish Marks.

This comprehensive work on the mammals of Finland is largely the result of field studies made over a ten-year period by Lauri Siivonen. Unpublished data have been contributed by other workers and use has been made of the information derived from the investigations of the Finnish Institute for Game Research. This is the second of a series of volumes on the fauna and flora of Finland, published by the Otava Company.

The introductory chapter is concerned with the general characteristics of the mammalian fauna of Finland from the Ice Age to the present, with particular reference to abundance, distribution, migration routes and early historical information.

The greater part of the book (pp. 28–712) is comprised of detailed accounts of species, including information on distribution, reproduction, movements, food habits and general ecology, prepared by Siivonen and several collaborators. This section is illustrated with about 575 photographs, nearly all of excellent quality, of which 25 are in color. Many aspects of the lives of Finnish mammals are portrayed in their natural habitats. There are 68 maps and numerous drawings.

The section on systematics (pp. 713–786) is prefaced by a discussion of the identification of mammals and of mammalogical techniques. Keys are provided for all species, morphological characteristics are illustrated by line drawings, and standard measurements are included in the detailed descriptions. The nomenclature closely follows that of Ellerman and Morrison-Scott (1951). The Finnish names of the mammals are used throughout the text, but a list including the technical and Swedish names is found on pages 788–791.

This list of 87 species includes those now extinct, those which have been introduced, and species which may be expected to occur in Finland. Several species new to Finland have been recorded since the last comprehensive work on Finnish mammals (cf. Kivirikko, 1940).

Unfortunately, as is true generally, the ranges of the larger carnivores in Finland have greatly diminished since 1880. The wolf, brown bear, wolverine and lynx are found now only in the remote parts of northeastern Finland. Several introduced species, such as the North American beaver which interbreeds freely with the indigenous form, have become established and are extending their ranges.

Siivonen's book is an important contribution, providing valuable information on the natural history of boreal mammals, and furnishing an excellent guide to the mammals of the Fennoscandian region. Mammalogists not literate in Finnish can nevertheless use the systematic section if only a few standard terms are learned, since the diagnostic characteristics of the more difficult groups are quite clearly figured. It is hoped, however, that this book can later be published in German or English.—ROBERT RAUSCH.

Cabrera, Angel. CATALOGO DE LOS MAMIFEROS DE AMERICA DEL SUR. I. (Metatheria-Unguiculata-Carnivora). Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoologicas, Vol. 4, No. 1, pp. iv + 307, 27 March 1958. [In Spanish.]

Cabrera's long-awaited check list of South American Recent mammals is now, at least in part, a reality. It is an excellent work that fills a large gap in mammalian literature. This first volume includes the marsupials, insectivores, bats, primates, edentates and carnivores. The remaining orders, together with additions and corrections, will appear in a subsequent volume or volumes.

The format provides for easy reference. Each entry is identified by the valid scientific name in boldface type and is set apart from other entries by extra space. Each page has ample margin all around for annotations. Species and subspecies are listed alphabetically under genera or subgenera. For each form there are full synonymy, geographical distribution, type locality and (where necessary) terse taxonomic and nomenclatorial notes.

The area included is the continent of South America to the Colombia-Panama boundary, the Galapagos Islands, Venezuelan and other islands belonging politically to South American countries, and the contiguous seas. The full geographic range of a form is given even if it extends beyond these boundaries. However, the Falkland Islands and the distinctly South American islands of Curaçao, Aruba, Bonaire, Trinidad and Tobago are omitted; forms endemic to the latter islands do not appear in either the North American or the South American check lists.

Cabrera has rescued many nominal genera from the premature synonymy to which Simpson (Bull. Amer. Mus. Nat. Hist., Vol. 85, 1945) relegated them. On the other hand, he has substantiated some of Simpson's assertions. One new name is proposed: *Hesperomyotis*, a subgenus for *Myotis simus* Thomas.

This work is particularly important to North American specialists because it attempts for the first time a large-scale synthesis of the North and South American mammalian faunas. Until now we have gotten along with one set of names north of the Colombia-Panama boundary and another set south of it, although that boundary is not a biogeographic barrier. Unfortunately Cabrera had to base his synthesis largely on literature rather than on direct comparison of pertinent specimens. However, the probability is great that his estimates were correct in most instances.

Name combinations that differ from those for the same taxa in the North American list of Miller and Kellogg (Bull. U. S. Nat. Mus., 205, 1955), with the older combinations in parentheses, are as follows:

Marmosa robinsoni isthmica Goldman (*Marmosa mitis isthmica* Goldman). By inference, other North American races of *mitis* would also become races of *robinsoni*.

Didelphis marsupialis marsupialis Linnaeus (*D. m. battyi* Thomas, *D. m. etensis* J. A. Allen, *D. m. insularis* J. A. Allen, *D. m. particeps* Goldman). This combination has already been used by Hershkovitz (Fieldiana-Zool., 31: 550, 1951) for *D. m. etensis*.

Chironectes minimus panamensis Goldman (*Chironectes panamensis* Goldman).

Noctilio labialis labialis Kerr (*Noctilio labialis minor* Osgood).

Tonatia sylvicola sylvicola D'Orbigny (*Tonatia amblyotis* Wagner).

Vampyressa thyone Thomas (*Vampyressa minuta* Miller).

Thyroptera tricolor albiventer Tomes (*Thyroptera tricolor albigula* G. M. Allen).

Eumops abrasus Temminck (*Eumops abrasus milleri* J. A. Allen).

Cebus capucinus capucinus Linnaeus (*Cebus capucinus imitator* Thomas).

Bradypus infuscatus ephippiger Philippi (*Bradypus griseus ignavus* Goldman). By inference therefore: *Bradypus infuscatus griseus* Gray (*Bradypus griseus griseus* Gray).

Choloepus hoffmanni hoffmanni Peters (*Choloepus hoffmanni* Peters).

Spethos venaticus panamensis Goldman (*Icticyon panamensis* Goldman). This combination has already been used by Hershkovitz (Novedades Colombianas, 3: 161, 1957).

Potos flavus megalotus Martin (*Potos flavus isthmicus* Goldman).

Bassaricyon gabbii medius Thomas (*Bassaricyon gabbii orinomus* Goldman).

Galictis vittata canaster Nelson (*Grison canaster* Nelson).

Eira barbara sinuensis Humboldt (*Tayra barbara biologiae* Thomas).

Lutra annectens colombiana J. A. Allen (*Lutra annectens repanda* Goldman).

Felis pardalis aequatorialis Mearns (*Felis pardalis mearnsi* J. A. Allen).

—CHARLES O. HANDLEY, JR.

Mohr, Erna. SÄUGETIERE. Color plates by W. Eigener, F. Murr, K. Grossman and H. Vogel, with descriptive text; contents and front matter in 15 separate pages. Kronen-Verlag Erich Cramer, Hamburg. To be issued in six installments, 1958–1960. Price, $35.94.

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individual plates, representing all 18 orders and 70 families of living mammals. Several of the lesser-known families of marsupials, insectivores, bats and rodents have necessarily been omitted. Particularly well represented are the cats, mice, mustelids and bovids. Many of the species illustrated are familiar in zoological parks, but they are shown here with a suggestion of their native habitats.

This is one of a Series of Natural History Plates already including sets on the trees and shrubs, flowers, insects and birds of Middle Europe. This series has been ably compiled by Erna Mohr, of the Zoological Institute and Museum of the University of Hamburg, with the collaboration of Theodor Haltenorth, of the Zoological Collection of the Bavarian States in Munich. On the reverse of each plate, printed lightly in sepia, is a brief description (in German) of the animal's haunts and habits, with notes on such topics as relationships, social behavior, feeding and breeding, longevity, distribution, structural traits and economic significance. Vernacular names are given, as well as the classification from species to order (following Simpson, 1945). These sketches seem singularly appropriate for use by graduate students faced with a foreign language examination. Provided with each subscription is an attractive and practical portfolio designed to hold all 192 plates, each approximately 7⅛ × 10⅛ inches.

In the first two issues at hand (64 plates) most of the paintings are from the brush of Eigener. He has caught beautifully, not only the color and texture, but the spirit of his subjects. His wolf is as alert as any wild dog; one half expects the zebra to toss its head and whinny, or the skunk to reach out and dig up a grub; the white-tailed deer might have just stepped forth from a snowy wood; and the handsome sable antelope is boldly rendered with faithful attention to all its fine points. In comparison to these and most others, a few are lacking in some subtle way; the shoulders seem much too humped for the fleet cheetah, the head and body too chunky for the jaguar; the leopard seal has the diabolical grin of the serpent in Eden; and certainly no red deer has such an elongate face as the doe illustrated. But these few shortcomings are truly the exceptions. The figures by Murr are done with a softer touch, a skillful blending of tones which, at a short distance, is amazingly convincing. His chamois, reproduced on an accompanying page, is a typical example. His weasels, in winter and summer, and his tree dormouse are especially appealing. The mountain goat, bounding down an alpine slope, seems less realistic—reminiscent of a skier executing a geländesprung! Grossman has specialized in the smaller mammals, and his shrew, mole and several mice are done with great feeling and attention to detail. One might wish that the plates of black rat (with corn) and Norway rat (with apples) had been devoted instead to more deserving creatures. No examples of Vogel's work appear in these initial sets.

Simply perusing these pictures will bring hours of enjoyment. They are not only attractive artistically, but accurate scientifically, with few exceptions. They should appeal to the biologist, the aesthete and the dilettante alike. Certainly they would grace the walls or shelves of any mammalogist with a broader interest than in the fauna of his own back forty.—RICHARD H. MANVILLE.

RECENT LITERATURE

(Prepared by the Committee on Bibliography)

[Reprints of this bibliographic section may be purchased from the Secretary-Treasurer. However, the Society cannot furnish reprints of the individual publications listed.]

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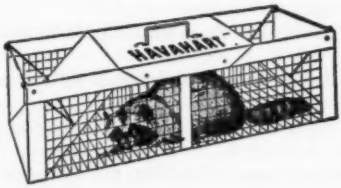

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COMMENTS AND NEWS

NOTICE OF ANNUAL MEETING

The Thirty-ninth Annual Meeting of the Society will be held in Washington, D. C., on June 22–24, 1959. Official headquarters will be the Harrington Hotel, where the Directors' meeting will be held at 8:00 PM on June 21. Registration and regular sessions will begin on Monday morning, June 22, at the National Museum. The Chairman of the local committee on arrangements is Miss Viola S. Schantz.

Titles for papers should be submitted to the Secretary-Treasurer, Dr. Bryan P. Glass. The deadline is May 1, but since only approximately 30 papers will be scheduled on the program, it is urged that titles, estimates of time and equipment needed be sent in at an early date. Papers to be considered for an honorarium and resolutions proposed for action should be submitted early (see below).

Members desiring accommodations during the meetings should make reservations directly with the resort concerned. Since the tourist season will be in full swing, arrangements should be made several months in advance. The Harrington Hotel is conveniently located at 11th and E Streets, N.W., Washington 4, D. C. Minimum daily rates for rooms with bath are as follows: single, $6.00; double bed, $8.00; twin beds, $9.50; three or four to a room, $12.00. On nearby Hains Point is the Potomac Park Motor Court, operated under the National Park Service, for those desiring unpretentious but adequate accommodations. Scores of motor courts, all with air-conditioning, private bath and television, are located about the metropolitan area. All are close to restaurants and bus transportation to the District. Several facilities which are recommended are the following (distances are from the National Museum; rates are by the day):

BETHESDAN MOTOR-HOTEL, 7740 Wisconsin Ave., Bethesda 14, Md. (8.5 mi., 73 rooms, swimming pool; single $8, double $10 and up)

IWO JIMA MOTOR HOTEL, 1501 Arlington Blvd., Arlington, Va. (3.3 mi., 74 rooms, swimming pool; single $8–10, double $10–14)

MARRIOTT MOTOR HOTEL, Twin Bridges on U.S. 1, Washington 1, D.C. (2.4 mi., 375 rooms, swimming pool; single $9–11, double $12–14 and up)

MOTEL FIFTY, 1601 Arlington Blvd., Arlington, Va. (3.4 mi., 38 rooms; double $10 and up)

SOUTH GATE MOTOR HOTEL, 2480 S. Glebe Rd., Arlington, Va. (5.4 mi., 210 rooms, swimming pool; single $8, double $10 and up)

VIRGINIA MOTEL, 700 N. Washington St., Alexandria, Va. (6.8 mi., 24 rooms; double $10 and up)

PRESIDENTIAL GARDENS, Mt. Vernon Ave. and Russell Rd., Alexandria, Va. (5.6 mi., 387 completely furnished housekeeping suites; double $10, four persons $14 and up)

POTOMAC PARK MOTOR COURT, East Potomac Park, Washington 4, D. C. (1.5 mi., 68 cottages with or without bath, single $1.50, double $3 and up; special rates for parties of ten or more; trailer park and camping facilities; make reservations early).

HONORARIA

Two honoraria are available each year for young mammalogists who have not obtained the Ph.D. degree. These honoraria carry a stipend of $100.00 each to help defray the expenses of travel to the annual meeting for the presentation of the paper. Our next meetings will be held in Washington, D.C., June 22–24, 1959. Entries should be submitted to Dr. Stephen D. Durrant, Department of Zoology, University of Utah, Salt Lake City, Utah, before April 1, 1959.

RESOLUTIONS

Members having resolutions intended for action by the Society at its next annual meeting are urged to submit them to the Resolutions Committee at the earliest opportunity. The committee is anxious to submit the proposals to the members prior to the meeting but can do so only if they receive such proposals at an early date. May 1, 1959, has been set as a deadline. Proposed resolutions should be sent to the Committee Chairman, Dr. Keith R. Kelson, National Science Foundation, Washington 25, D. C.

PROPOSED AMENDMENT OF BYLAWS

In the course of preparing a revised copy of the BYLAWS AND RULES for publication in the Journal as directed by the Board of Directors at the annual meeting in June, 1958, several discrepancies have been uncovered. At the annual meeting in June, 1951, the Society adopted the recommendation of the Board of Directors that a new grade, Emeritus Membership, be established and that any necessary changes in the Bylaws be made to expedite this. Since these changes were overlooked at the time it is proposed that Section 1 of Article II be amended to read as follows:

SEC. 1. The Society shall consist of Members, Honorary Members, Patrons and Emeritus Members.

To explain the emeritus class of membership it is recommended that Section 5 be added to Article II to read as follows:

SEC. 5. Individuals who have been for twenty-five (25) years members in good standing of the American Society of Mammalogists shall be eligible for Emeritus Membership at their request and shall be exempt from dues. Such membership *will not carry with it* the right to vote, nor the right to receive the Journal free. When a member is eligible for Emeritus Membership, and is in arrears for dues, the Secretary-Treasurer shall notify the member, indicating that it is necessary for him to request such change in his membership rank. At each annual meeting the Secretary-Treasurer shall report to the Board of Directors, for their approval, the names of members who are to be added to the Emeritus Membership List.

Since the executive officer of the Society, the Secretary-Treasurer, is appointed by the Directors, unless 20 per cent of the members in good standing at any annual stated meeting require a ballot submitted to them for approval or disapproval of the incumbent, it is proposed that Section 2 of Article II be amended to read as follows:

SEC. 2. Any person may become a Member upon recommendation of two Members and election at the next annual stated meeting, or by special election at other times by a two-thirds vote of the Directors (which may be obtained by correspondence). Members are entitled to vote for elective officers and Directors at large, and to receive the serial publication of the Society.

CALIFORNIA BIBLIOGRAPHY

A recent publication, "An Annotated Bibliography of Economically Important Species of California Fish and Game," lists various research papers on 144 species, including 15 of mammals. Copies are available in limited numbers, without charge, from the office of the California Assembly Interim Committee on Fish and Game, Room 3111, State Capitol Annex, Sacramento.

THE RECENT ZOOLOGICAL CONGRESS

The 15th International Congress of Zoology, held last year, attracted to London over 1,900 workers in various branches of animal science. Commenting on the meetings, W. R. Duryee reported (Science, 128: 1092; 1958) that "Taxonomists will be heartened to learn of the progress made by the International Commission for Zoological Nomenclature—progress which has led to the establishment of a permanent body to consider conflicts in terminology and classification. A heavy program of taxonomic recommendations and changes was accomplished in the week preceding, and during the congress. Nevertheless, the numerous wrangles over minutiae of nomenclature must have caused Darwin to turn over in his grave. Experimental zoologists seem to prefer to go calmly ahead, leaving systematics to a vociferous minority." In 1963 the next congress will be held in this country.

UNIQUE NEW JOURNAL

The Wildlife Disease Association, organized in 1951, now has a membership of nearly 300 whose interests are "concerned with the parasites, diseases, physiology, and other factors related to health and survival of wild animals, including those in captivity, their effects upon wild populations, and their direct and indirect relationships to man." In launching its new quarterly publication, WILDLIFE DISEASE, for an experimental period of three years, the Association pioneered in recent weeks in the medium of microform. Sixteen 3 × 5 cards will constitute an annual volume. Each card, besides a citation in conventional type, will contain a maximum of 47 pages, with photographic and other illustrations. The material can be read with the aid of a dissecting or stereoscopic microscope or with various readers currently on the market from $3.00 to $25.00. Members will receive the quarterly issues of Microcards, plus a leaflet in macroprint containing abstracts of the manuscripts, as well as the organization's Newsletter issued irregularly about four times per year. Annual dues are $1.00. Address applications to Dr. Carlton M. Herman, Chairman, Wildlife Disease Association, Patuxent Research Refuge, Laurel, Maryland.

PHOTOGRAPHS AVAILABLE

Mammalogists who would like to have living wild small mammals photographed for them without cost are invited to communicate with Ernest P. Walker (3016 Tilden Street, N.W., Washington 8, D.C.) who is working on the research and writing project, "Genera of Recent Mammals of the World." Persons could bring specimens to the Washington meeting or send them at some mutually convenient time, but no specimen should be sent without prior arrangements.

PHOTOGRAPH NEEDED

The Society is anxious to obtain a portrait of Marcus Ward Lyon, Jr. It is requested that anyone having or knowing the location of such a photograph please contact the Secretary-Treasurer.

NEW LIGHT ON ANCIENT SLOTH

During the Pleistocene, giant ground sloths ranged from Alaska to Cape Horn. In 1936, remains of one plant-eating, bear-like creature (*Nothrotherium shastense*)—including hair, hide, parts of the internal organs and skeleton—were discovered in Rampart Cave in the lower Grand Canyon, 4,000 feet below the rim. Recently Paul S. Martin and Dick Shutler, Jr., of the University of Arizona Geochronology Laboratories, reported further findings from Rampart Cave. The age of the plentiful sloth droppings, as determined by the Carbon 14 carbon dioxide gas counting method, indicate that the animal inhabited the cave between 10,000 and 35,500 years ago, not necessarily continuously. Analysis of pollen grains, which passed relatively unchanged through the digestive tract of the sloth, indicate that 12,000 years ago the creature lived in a cooler, moister environment, eating pine, juniper and sagebrush. Its environment 35,500 years ago, however, was much like that of the present—and of 10,000 years ago, when the sloth disappeared. It was dry and hot, and the pollen was dominated by composites, such as might be found in the area today. There is no evidence of man's having shared Rampart Cave with the sloth, nor of his displacing the sloth from the cave.

ADDRESSES UNKNOWN

Several of our members are at present unaccounted for and their mail has been returned for lack of a correct address. The Secretary-Treasurer will appreciate word from anyone who can advise as to the whereabouts of the following persons, listed with their last-known residence: Paul S. Eskridge, *Fort Collins, Colo.*; Duncan MacDonald, *St. Paul, Minn.*; Huey W. Metts, Jr., *Opelika, Ala.*; Carmie Ann Perrotta, *Kingston, Ont.*; Bill T. Ridgeway, *Wichita, Kans.*

CORRECTION

In Vol. 39, No. 4, p. 516, line 3 from bottom: for *humidity* read *ammonia.*

DEATHS REPORTED

Alex. W. Blain, December 14, 1958
Robert T. Moore, October 30, 1958
John T. Nichols, Charter Member, November 10, 1958
Edward L. Rabb, August 27, 1958
Clarence R. Shoemaker, Charter Member, December 28, 1958
Malcolm R. Thorpe, November, 1958.

PERSONAL NOTICES

This space is available to members of the Society for brief notices of interest to mammalogists. Copy should be sent to the editor by the 10th of the month preceding publication. Rates for single insertion are 25 cents per line or portion thereof. Bills will be rendered following publication.

FOR SALE—*Japanese "Mist" Bat Nets.* Send for price list. W. B. Davis, 254 F.E., College Station, Texas.

FOR SALE—*Live desert rodents.* Send for information and price list. Keith E. Justice, 44 W. Rillito St., Tucson, Arizona.

WANTED—*Preserved specimens,* just hatched or born, full term; all species; identified; maximum 12 hours. David Wetherbee, Hampton, Connecticut.

KEY TO THE SKULLS OF NORTH AMERICAN MAMMALS, by Bryan P. Glass, has been reprinted and may be ordered from the Research Foundation, Oklahoma State University, Stillwater, Oklahoma. Price $2.00 as in the past.

FOR *Sherman Live Traps* write H. B. Sherman, P.O. Box 683, De Land, Florida.

FOR SALE—*Transactions San Diego Society of Natural History,* complete set, Vols. 1–11 with Vol. 12 in progress, newly bound in blue buckram, $125. L. M. Huey, Natural History Museum, Balboa Park, San Diego 1, Calif.

POSITION WANTED—*Teaching and research.* M.A. in field zoology; qualified in general biology, zoology, ornithology, mammalogy, natural history and conservation, also much library experience in these fields. Seacoast or Southwest preferred, but any offer earnestly considered; available summer or fall 1959. Daniel McKinley, Dept. Biology, Bowdoin College, Brunswick, Maine.

FOR SALE—Packard, Cave fauna N. Am., $7.50; Allen, Whalebone whales N. Eng., $7.50; J. A. Allen, Smaller spotted cats, $2.50; N. Am. opossums, $2; Kellogg, Tenn. mammals, $1; Miller, Families and genera of bats, $5; M. and Allen, Bats Myotis and Pizonyx, $5; H. Allen, Bats N. Am., $4; Osgood, Papers on mammalogy, $4; Poole and Schantz, Catalog type specimens, $4; Vladykov, Marsouin blanc, nourriture mars. blanc, $2 ea.; Tate, Mammals E. Asia, $4; Carter, Hill, Tate, Mammals Pacific, $3; Anderson, Canadian Recent mammals, $2.50; Mearns, Mammals Mexican border, $7.50; Philippines—Hollister, 1913, $1; Miller, 1910, $1; Mearns, 1905, $1; Barbour, Lawrence, Peters, 1939, $1.50; de Beer, Vert. Zoology, $5. Postage prepaid. *Wanted:* Grinnell, Storer, Animals Yosemite; Dill, Life, heat, altitude. Raymond J. Hock, Arctic Aeromedical Lab, APO 731, Seattle, Wash.